What drives invertebrate communities in a chalk stream: from trophic relationships to allometric scaling

By

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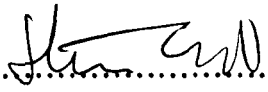
"I  *.....hereby declare all the work*

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ABSTRACT

Despite a slow start freshwater meiofauna research is now gathering pace. Evidence is accumulating which indicates the importance of their inclusion in lotic metazoan studies. Here I contribute towards this research effort by conducting an investigation of meiofauna and macrofauna from a chalk stream.

I sampled meiofauna for a 19 month period, and macrofauna for a 12 month period between April 2004 and October 2005 from the subsurface, macrophyte stands and gravel beds. The chalk stream community was highly diverse with 57 taxa identified from the subsurface and 186 from the benthos. Meiofauna outnumbered macrofauna in all habitats in terms of density. Both meio- and macroinvertebrates preferred macrophyte stands over gravel beds as habitat, indicated by higher densities, biomass and species richness. Species-abundance relationships and density-size spectra indicated the invertebrate assemblages of the benthos to be stable over the period of the study as patterns varied little between sampling months and habitats. Production and standing biomass were dominated by the macroinvertebrates which suggests meiofauna had a limited role within functioning of the stream. However, gut content data indicated meiofauna may play an important trophic role, linking basal resources and top consumers. Combined gut content and stable isotope analysis suggested a strong pattern of generalist feeding throughout the whole spectrum of body size in the community, rejecting the concept of functional feeding groups. Predominance of generalist feeding also suggested a large number of weak interactions in food webs. While higher species richness lower in food webs indicated greater functional redundancy of lower trophic levels.

Density-body size distributions were shallow with a biased distribution of energy towards larger size classes. Moreover, testing of production, standing biomass and P/B body size allometry was inconclusive with regards to theoretical predictions. The

interrelationship of biodiversity, stability, and trophic dynamics, with body size determine the structure and dynamics of the chalk stream community, not metabolism.

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CHAPTER 1: GENERAL INTRODUCTION

Meiofauna, defined by Fenchel (1978) as metazoans retained on a 42 μm sieve and passing through a 500 μm sieve have traditionally been overlooked in many freshwater studies by ecologists. Various reasons have been cited for this oversight including a lack of taxonomic expertise and the misleading notion that small size negates the possibility of meiofauna species exerting any significant impact on systems (Robertson *et al.* 2000). However, by far the most significant hindrance has been the historical tendency for aquatic ecologists to use sampling apparatus with mesh sizes of 250 μm or greater. These mesh sizes are only adequate for investigations of large macrofaunal taxa defined as individuals being retained by a 500 μm sieve.

The importance of studying meiofauna and macrofauna simultaneously is well established in marine research (McIntyre, 1969; Austin & Widdicombe, 2006) and it has become increasingly common practice in freshwater studies in recent years (Dole-Olivier *et al.* 1997; Schmid-Araya, 1997; Malard *et al.* 2003; Olsen & Townsend, 2003; Stead *et al.* 2003). Many macrofauna taxa particularly species of Insecta and Oligochaeta begin their life cycles as temporary meiofauna. Therefore, sampling both size classes of invertebrate simultaneously has the obvious benefit of including all the life stages of these temporary taxa in investigations. Furthermore, permanent taxa such as copepods, ostracods, and nematodes, complete their entire life cycle within meiofaunal size classes being completely missed by studies with inadequate sampling equipment.

Permanent meiofauna taxa contribute between 58% and 81% of total freshwater invertebrate species richness in some European streams (Robertson *et al.* 2000). As a group, meiofauna have been recorded reaching densities between 100,000 and 443,000 ind. m^{-2} (Bott and Borchardt, 1999; Stead *et al.* 2003). Consequently, the omission of meiofauna

may have seriously underestimated invertebrate species richness, densities, biomass, and production in many systems (Hakenkamp and Palmer, 2000; Stead *et al.* 2003). Recent studies of disturbance response, production, trophic interactions, and habitat types have all highlighted the importance of including meiofauna to enhance our understanding of lotic ecosystem structure and function (Dole-Olivier *et al.* 1997; Hakenkamp and Palmer 2000; Schmid-Araya *et al.* 2002; Stead *et al.* 2005*a*; Stead *et al.* 2005*b*).

With the exception of Bird (1982), meiofauna have been almost completely ignored in chalk stream studies despite a considerable research effort on the macrofauna (Whitehead, 1935; Harrod, 1964; Welton, 1979; Welton *et al.* 1983; Wright, 1984; Mann *et al.* 1989; Pinder, 1992; Wright and Symes, 1999; Harrison *et al.* 2005). The following contains a synopsis of current knowledge on chalk stream invertebrate assemblages, meiofauna generally, and meiofauna's context within ecological research topics. Brief summaries describing data collected and ecological research topics to which they are related are then provided in separate thesis chapters.

Chalk streams habitats – density and species richness

The most common major habitat types within chalk streams are macrophyte stands, gravel beds, and the subsurface or hyporheic zone. The hyporheic zone first recognised by Orghidan (1959) can broadly be defined as the area directly below and adjacent to the stream channel which receives inputs of water from the surface and subsurface (groundwater). A large number of studies have been published, demonstrating the importance of the hyporheic zone to lotic invertebrates (Marmonier and Creuzé des Châtelliers, 1991; Brunke and Gonser, 1997; Franken *et al.* 2001; Malard *et al.* 2003; Olsen and Townsend, 2003). However, there has been only one study concerning the oligochaete,

Propappus volki Michaelsen, within the subsurface of a chalk stream (Bird, 1982) where low densities down to a depth of 40 cm were found.

Across different studies, a variable depth distribution pattern has been documented spatially and temporally for specific taxa and whole hyporheic invertebrate communities (Dole-Olivier *et al.* 1997; Schmid-Araya, 1997; Franken *et al.* 2001; Stead *et al.* 2004). Where hyporheic invertebrate densities are high and distributions extensive the fauna may play an important role in providing extra food for benthic taxa (Huryn, 1996). Moreover, the importance of hyporheic taxa to ecosystem function remains largely unstudied (Hakenkamp and Palmer, 2000). Hyporheic taxa may contribute significantly to invertebrate production and ecosystem respiration in some environments (Pusch, 1996; Naegeli and Uehlinger, 1997; Boulton *et al.* 1998). Consequently, the hyporheic zone may form an understudied but yet important habitat within chalk stream ecosystems.

Of the two main benthic habitats found in chalk streams, macrophyte stands and gravel beds, the former tend to hold the highest diversity, abundance and biomass of macroinvertebrates (Harrod, 1964; Wright, 1984; Pinder, 1992; Wright and Symes, 1999). Investigations of higher plant lotic macrophytes in chalk streams have demonstrated they can significantly alter water flows rates leading to deposition of sediment and organic matter into concentrated patches (Cotton *et al.* 2006). This potentially increased habitable area and food availability may explain differences in the macroinvertebrate distributions between benthic habitats, but association with macrophytes may also afford protection from predation (Harrison *et al.* 2005).

Within lentic habitats higher densities of meiofauna have been reported from higher plant macrophyte stands (Paterson, 1993; Silver & Cowell, 1993). However, within lotic environments the only investigations of macrophytes have concentrated on lower plant mosses (Suren, 1992; Linhart *et al.* 2002; Fontaneto *et al.* 2005). These studies concluded

macrophytes were more important than gravel beds in supporting higher densities and species richness of meiofauna. Consequently, there is a potentially significant role for higher plant lotic macrophyte stands to play in providing important habitat for lotic meiofauna generally, and particularly in chalk streams.

Standing biomass and production

Welton (1979) estimated the production of *Gammarus pulex* (L.) from a chalk stream while Baldock *et al.* (1983) investigated the production of ciliates. However, biomass and production studies are rare for lotic meiofauna and no estimates have been made in chalk streams. Within an acid stream, Stead *et al.* (2003) found significantly higher densities of meiofauna than macrofauna and a relatively even contribution to total biomass of both size classes. Stead *et al.* (2005*a*) reported a 51% contribution of meiofauna to total secondary production. A range from 0.01% to 22% for the contribution of meiofauna to total biomass has been reported elsewhere, along with an even larger range of between 0.7% and 52% for the contribution to total secondary production (Hakenkamp *et al.* 2002). Various hypotheses have been suggested for explaining the variable contribution of meiofauna to total biomass, secondary production, and consequently ecosystem function. These include changing taxonomic composition (Hakenkamp and Morin, 2000) and the influence of sediment grain size (Hakenkamp and Palmer, 2000). Investigations in other lotic ecosystem types such as chalk streams may provide insights into if and when meiofauna are important to lotic ecosystem function.

Density and body size

Of all the different allometric relationships found, the species density-body size relationship has been subject to some of the most intense research with it now being well established

that density decreases with increasing body size (Damuth, 1981; Peters, 1983; Peters and Wassenberg, 1983; Blackburn and Gaston, 1999). There are competing hypotheses attempting to predict and explain the form of this relationship including: metabolic constraints (Damuth, 1981; Rinaldo *et al.* 2002; Brown and Gillooly, 2003; Marquet *et al.* 2005), variable species richness between body sizes (May, 1986), and effects of habitat architecture (Holling, 1992; Schmid, 2000). Investigations of the temporal aspect of body size distributions remain largely unexplored with a few exceptions (Schmid *et al.* 2002; Stead *et al.* 2005*b*). Furthermore, only a few analyses of lotic invertebrate communities including both meiofauna and macrofauna have been conducted, with mixed results (Schmid, 2000; Schmid *et al.* 2002; Stead *et al.* 2005*b*). Makarieva *et al.* (2004) suggested that conflicting results of investigations into the size distributions of habitats such as streams and rivers may be due to these systems suffering high natural levels of disturbance. However, no investigations have been carried out in chalk streams which, due to their unusual catchment geology and porosity, possess stable discharge and thermal regimes (Prenda, *et al.* 1997; Pretty *et al.* 2006).

Production, biomass and production/biomass allometry

Few investigations of P/B-body size allometry have been conducted since the seminal paper of Banse and Mosher (1980) despite the obvious commonality in terms of the currency, 'energy', being investigated. Some advances have led to continuity between theoretical predictions and the scaling of P/B with body size (Humphreys, 1979; Schwinghamer *et al.* 1986; Dickie *et al.* 1987), and production (Ernest *et al.* 2003). However, there have been no studies investigating body size allometry of standing biomass which has been strongly positively correlated with production in freshwater and marine systems (Plante and Downing, 1989; Morin and Bourassa, 1992; Benke, 1993; Cusson and Bourget, 2005). The

three notable investigations of production and biomass allometry in freshwater taxa did not include meiofauna (Plante and Downing, 1989; Morin and Bourassa, 1992; Benke, 1993). The affects of including meiofauna on the shape of the relationships between production, standing biomass, and P/B for freshwater taxa is unknown. In marine systems they had a unifying effect upon theoretical predictions and empirical data (Schwinghamer *et al.* 1986; Dickie *et al.* 1987).

Trophic interactions and meiofauna

Although the macroinvertebrate fauna of chalk streams is well described (Wright and Symes, 1999), as is the feeding habits of fish commonly found in these habitats (Welton *et al.* 1983; Mann *et al.* 1989), no attempts at constructing invertebrate food webs have been made. Moreover, diatoms which are cosmopolitan in distribution and highly speciose in British rivers (Kelly, 2000) have largely been ignored or left unresolved in current publications of freshwater food webs. Meiofauna have also been largely ignored even though they have been shown to occupy an important intermediate role in food webs consuming basal resources, small microfauna, and other meiofauna, and in turn falling prey to larger invertebrates and fish (Schmid-Araya and Schmid, 2000; Schmid-Araya *et al.* 2002).

Natural abundance stable isotope analysis and meiofauna

With advances in analytical chemistry techniques it is now possible to analyse very small tissue samples sizes (Carman and Fry, 2002; Houghton *et al.* 2002). Successful natural abundance stable isotope analyses of meiofauna have taken place for marine and brackish environments: demonstrating variability between species seasonally (Carman and Fry, 2002), preferential feeding of food resources (Riera *et al.* 1996), and providing evidence for

a relationship between population stability and diet spectra (Romanuk *et al.* 2006). Only one lotic invertebrate study including meiofauna has taken place which used isotopic tracers (Hall and Meyer, 1998). In this study benthic harpacticoid copepods were shown to gain over 50% of their total dietary carbon requirements from bacteria. Consequently, the potential of natural abundance stable isotope techniques in providing new insights into the feeding and trophic relationships of lotic meiofauna remains unexplored.

The following objectives are addressed in this thesis:

Chapter 2. The first simultaneous assessment of the whole meio- and macrofauna community from within the hyporheic zone and two benthic habitats, macrophyte stands and gravel beds, of a chalk stream over one year was conducted. I describe the distribution of hyporheic invertebrate densities, as well as the density and biomass of meiofaunal and macrofaunal assemblages associated with the benthic macrophyte stands and gravel beds. I investigate the species composition of the invertebrate communities associated with the two benthic habitats. The objectives were to examine the depth distribution of both macro- and meiofauna within the hyporheic zone, compare the density and biomass of meiofauna with that of macrofauna between macrophyte stands and gravel beds, and examine seasonal differences in species richness of the invertebrate community of the two benthic habitats.

Chapter 3. Because of the high reported densities and the habitat differences, the aim of this chapter was to estimate and evaluate the whole metazoan invertebrate secondary production for macrophyte stands and gravel beds within a chalk stream. A unique estimate of total secondary production and standing biomass for the

whole invertebrate assemblage of a chalk stream is presented. The objective was to directly compare annual production and standing biomass of meiofauna and macrofauna, and dominant invertebrate groups, between the macrophyte stands and gravel beds.

Chapter 4. A complex stream food web including highly resolved basal and intermediate species is described, with general food web properties. Seasonal changes and effects of varying taxonomic resolution are investigated. Natural abundance stable isotope analysis of lotic benthic meiofauna was performed with an assessment of functional feeding groups. The objectives were to resolve taxonomically challenging groups such as diatoms and meiofauna to genus and species wherever possible providing one of the most complete descriptions of a stream invertebrate food web to date. Also, too explore the effects of changing taxonomic resolution on this food web and the impact of resolving taxonomically challenging groups. Finally, to provide the first dual gut content and stable isotope analysis of meiofauna assessing the value of classifying taxa into functional feeding groups. A new simplified lotic food web representative of the invertebrate community found in a chalk stream system is proposed.

Chapter 5. In this chapter I construct density-size spectra, density-size distributions, as well as species-size distribution. The two benthic habitat types, macrophyte stands and gravel beds are compared temporally and conformance to theoretical predictions relating to habitat architecture and metabolic constraints are assessed. Specifically spatial and temporal variation in density-size spectra is examined, along with tests to determine whether there are seasonal or between habitat differences in density-body size relationships. I perform tests of goodness of fit to any of the hypothetical scaling values of -3/4, -2/3 and -1

using Ordinary Least Squares (OLS) and -1 with Reduced Major Axis (RMA) regression methods. I also test the prediction of May (1986) that species richness increases with decreasing body size.

Chapter 6. In this chapter I extend the analysis of production, standing biomass, and P/B from freshwater macrofauna over meiofaunal size invertebrates for the first time. Unlike all previous analyses a large number of observations are used from data collected with a standard sampling protocol and production estimation method. My objectives were to rigorously test the theoretical exponents for production (3/4), standing biomass (0, 1/4) and P/B (-1/4) over a body size spectrum including both macrofauna and meiofauna.

CHAPTER 2: FROM MEIOFAUNA TO MACROFAUNA: DENSITY, BIOMASS, AND COMMUNITY STRUCTURE OF THE INVERTEBRATE ASSSEMBLAGE IN A CHALK STREAM

ABSTRACT

The whole metazoan community, meiofauna plus macrofauna, inhabiting the hyporheic zone, gravel beds and macrophyte stands, of a chalk stream were surveyed between April 2004 and March 2005. Invertebrate density, biomass, and species richness were compared between the two benthic habitats temporally.

A total of 57 invertebrate species was recorded within the hyporheic zone all with low densities. Meiofauna were significantly more numerous than the macrofauna with densities decreasing rapidly with depth from 10 cm (rmANOVA: $P < 0.01$). The stream benthos (185 species) was much more speciose than the hyporheos (57 species). Meiofauna were more numerous than macrofauna, but had lower total biomass. A significantly higher density and biomass of both groups was found associated with lotic macrophyte stands than bare gravel beds (rmANOVA: $P < 0.01$). Macrofauna and meiofauna showed synchronous increases in density during the summer during the growth period of lotic macrophytes. Rank-abundance analyses suggested significant seasonal changes in the invertebrate assemblage between the macrophyte stands and gravel beds.

These data suggest that hyporheic zones are of limited importance as utilisable habitat to invertebrate communities in chalk streams and rivers. Lotic macrophytes form the most important benthic habitat for meiofauna and macrofauna. Despite a large difference in size, both meiofauna and macrofauna responded similarly to changes in the benthic habitat caused by lotic macrophyte growth.

INTRODUCTION

Recent investigations of disturbance responses (Dole-Olivier *et al.* 1997), food web complexity (Schmid-Araya *et al.* 2002a), production (Stead *et al.* 2005a), density body-size distributions (Stead *et al.* 2005b) as well as studies in hyporheic zones (Hakenkamp and Palmer, 2000), highlight the importance of including meiofauna in the understanding of ecosystem functioning. Meiofauna defined by Fenchel (1978) as metazoans in the size range of 42 μm to 500 μm have traditionally been overlooked in freshwater studies resulting in a slow pace of research (Rundle *et al.* 2002). This oversight has been attributed to multiple factors among which lack of taxonomic expertise and inadequate mesh sizes of sampling equipment used are the most relevant, and have resulted in a possible underestimation of the importance of meiofauna to stream communities (Hakenkamp and Palmer, 2000; Stead *et al.* 2003).

The importance of studying meiofauna and macrofauna simultaneously has been well established in marine research for a number of years (McIntyre, 1969; Austin & Widdicombe, 2006). Studies combining meiofaunal and macrofaunal components of stream invertebrate communities have recently become more widespread with publications from gravel streams (Schmid-Araya, 1997; Malard *et al.* 2003; Olsen & Townsend, 2003), acid streams (Stead *et al.* 2003) and large lowland rivers (Dole-Olivier *et al.* 1997). To date there have been no investigations combining macrofauna and meiofauna within lowland chalk streams.

Within lowland chalk streams the three commonest habitat types are the hyporheic zone, benthic macrophyte stands and gravel beds. No single widely accepted definition of the hyporheic zone exists (Adkins and Winterbourn, 1999), however the hyporheic zone was first recognised by Orghidan (1959) and comprises the sediment beneath and adjacent to the river channel which receives water inputs from both the surface and subsurface

(groundwater). Reported vertical distribution patterns of hyporheic taxa seem to differ: a) density increased at depths of 15 cm in an acid stream (Stead *et al.* 2004) and at depths of 40 cm in a gravel stream (Schmid-Araya, 1997); but b) density decreased in other gravel streams (Franken *et al.* 2001). Taxa specific patterns have been found in lowland rivers, notably with significantly higher densities 2 m deep within the hyporheic zone (Dole-Olivier *et al.* 1997). In the only investigation of the hyporheos in a chalk stream, the oligochaete *Propappus volki* Michaelsen was found at low densities in the hyporheic zone down to a depth of 40 cm (Bird, 1982).

Numerous studies have been published on benthic macroinvertebrates in chalk streams and rivers dating back to Whitehead (1935). Densities of macroinvertebrate assemblages of macrophyte stands have been investigated (Harrod, 1964), along with comparisons of macroinvertebrate densities, diversity and predation rates between macrophyte stands and gravel beds (Wright and Symes, 1999; Harrison *et al.* 2005). Investigations between macrophyte stand and gravel bed habitats also included specific taxa such as the dipteran family Chironomidae (Wright, 1984; Pinder, 1992), whilst production and biomass estimates for the amphipod *Gammarus pulex* (L.) have been made (Welton, 1979).

To date there have been no studies of whole benthic communities of meiofaunal sized organisms in either gravel beds or macrophyte stands within chalk streams. The few studies of meiofauna inhabiting lotic macrophytes, have mainly concentrated on stream bryophyte communities (Suren, 1992; Linhart *et al.* 2002; Fontaneto *et al.* 2005). Fontaneto *et al.* (2005) found including bryophyte-associated meiofauna in community analyses could increase species richness even over small spatial scales of around a few metres within stream sites. Whilst Linhart *et al.* (2002) investigating a Czech river and Suren (1992)

investigating two New Zealand streams, both concluded that aquatic bryophytes are important in streams as they support higher numbers of meiofauna than gravel beds.

When simultaneously examining macro- and meiofauna in an acid stream, the Lone Oak, Stead *et al.* (2003) reported a significant contribution of meiofauna to benthic species richness (148 species out of a total of 163 species), meiofaunal densities between 2 and 22 times higher than that of the macrofauna, and a significant contribution from meiofauna to total benthic invertebrate biomass. Therefore these authors concluded that an omission of meiofauna has probably resulted in an underestimation of total benthic invertebrate density, biomass and species richness for chalk streams also.

In this chapter the apparent lack of published studies providing a simultaneous assessment of meiofauna and macrofauna within the hyporheic and benthic habitats of chalk streams is addressed. In particular the first comparison of a whole meiofauna community associated with gravel beds and lotic macrophyte stands dominated by higher plants within a chalk stream is conducted. The first objective was to examine the depth distribution of both macro- and meiofauna within the hyporheic zone during a year. Then the benthic density and biomass of both groups between gravel bed and macrophyte stands over a whole year was compared. Finally, seasonal differences in the species richness of the invertebrate community of the two benthic habitats were examined.

MATERIALS AND METHODS

Study Area

The River Lambourn drains a highly permeable Cretaceous chalk catchment (234km^2) of the Berkshire Downs, Southern England UK. The river is fed with groundwater from an aquifer which absorbs most rainfall in the catchment resulting in little overland flow and a stable discharge. Flow is intermittent in the upper reaches (7km), but is permanent for the

remaining length (18km) until the confluence with the River Kennet at Newbury (Fig. 1). There is only one surface tributary, the intermittent Winterbourne stream which confluences at Bagnor. Land use is dominated by agriculture and the river is hypernutrified, particularly with nitrate (Pretty *et al.* 2006).

The study area was an 80 m reach of the north-channel at Bagnor (SU 452 693), 10 m below the confluence of the Winterbourne stream (Figs. 1,2). Water entering the north-channel is controlled by a weir 100 m upstream of the study site. Channel width varies between 3 and 6 m, and the river is shallow with a maximum depth of 0.4 m. The immediate riparian vegetation on the right bank of the study site consisted of Salix *spp.* woodland and a wetland margin running the length of the left bank. Streambed characteristics at the study site were typical of this type of river: a stable discharge producing no well defined riffle-pool sequence. There was a gradual shift from coarser to finer sediments between areas of shallow fast flow to deeper slower flow. Main streambed heterogeneity was caused by growth of discontinuous stands of lotic macrophytes. No monocultural stands were found but *Ranunculus spp.*, *Berula erecta* (Hudson) Coville, and to a lesser extent *Callitriche spp.* were dominant.

Measurements of abiotic variables

Monthly measurements of pH, surface water temperature, and conductivity were taken from May 2004 until March 2005 with a Hanna combination meter (Hanna Instruments UK, Ltd). Monthly discharge was estimated from a cross-section at the top of the field site where water depth and flow velocity measurements were taken.

From August 2004 through March 2005 measurements of upwelling/downwelling water movements were taken with mini-piezometers using the method of Wagner and Bretschko (2003). Mini-piezometers were made from PVC tubing (length 1 m, inner

diameter ID 18 mm OD 28 mm,) and inserted into the streambed 1 m upstream from each stand-pipe at the field site. Mini-piezometer sampling depths replicated those of the corresponding stand-pipe traps (see experimental design). After installation each mini-piezometer was bailed with hose tubing to remove any water. Mini-pizeometers were then allowed 2 h to recharge before measurements of water level inside the mini-piezometer (h_p) and outside the mini-piezometer (h_s) were taken (see Fig. 3). Measurements of h_p were taken by placing a graduated dipstick with a buzzer that sounded on contact with water inside each mini-piezometer. Fast flows caused constant fluctuations in h_s so to increase accuracy of these measurements a bucket with the bottom removed was placed over each mini-piezometer which acted as a stilling well. Some h_s and h_p measurements were rechecked 3-4 h later to see if they had changed significantly.

The measurements of h_s, h_p, and piezometer depth into the streambed (d) were then used to estimate vertical hydraulic gradient (VHG) from each piezometer using the equation given by Dahm and Valett (1996);

$$\text{VHG} = \frac{h_s - h_p}{d}$$

VHG is a unit-less measure of pressure differences (Lee and Cherry, 1978) where positive values indicate upwelling subsurface water whilst negative values indicate downwelling surface water.

A thermocouple thermometer with a bare wire probe (model HI 91531K, Hanna Instruments Ltd, UK) was also used to measure ambient water temperature within each mini-piezometer. The difference in ambient water temperature between the surface and subsurface (particularly during summer and winter when maximum differences are found), can be used as a tracer to identify vertical water movements and the degree of mixing of the different water bodies.

Measurements of sediment organic content estimated as loss-on-ignition (LOI) were taken bimonthly from the modified Hess samples and seasonally from stand-pipe traps containing the invertebrates after these had been processed.

Experimental design

Quantitative samples were taken monthly at the streambed surface and within the hyporheic zone (subsurface) from April 2004 until March 2005. Stand-pipe traps were used to sample the subsurface, and a modified Hess sampler (surface area: 2.71 dm^2; mesh size 42 μm) to sample the streambed surface (see Fig. 4).

Each stand-pipe trap was made to the basic description of Bretschko & Klemens (1986) using PVC tubing 6 cm inner diameter and 170 cm length, with a circle of six catching holes (each 2.2 cm x 1 cm; total opening area 13.2 cm^2) positioned in a ring 20 cm from the base. A hard plastic cone (10 cm length, 8 cm width at base) attached to the bottom of each stand-pipe trap sealed them water tight from below, and also made installation easier by displacing sediment when they were driven into the streambed. Each stand-pipe trap was equipped with a water tight bung made of narrow plastic piping and foam pipe insulation that blocked the catching holes whilst not in use. A 10 cm deep sump was present within the bottom of each stand-pipe trap and was used to collect interstitial fauna, sediments and water when sampling. Stand-pipe traps were permanently installed and the interstitial habitat given one month to recover from this initial disturbance event before sampling commenced (Schmid-Araya, 1994).

To extract a sample, the bungs were pulled out of the stand-pipe traps with a hook fixed to a metal pole. As the bungs were removed from the stand-pipe traps, interstitial water, sediment, and any hyporheic fauna surrounding the catching holes were drawn into the sump. The sample was then removed with a pump which resembled an oversize syringe.

The pump was limited in its suction capacity by the length of tubing used to construct it and its efficiency. It therefore took an almost constant volume of sample equalling approximately 600 to 700 ml. After each sample was taken the stand-pipe trap bung was replaced, re-sealing the catching holes until the next sampling.

Stand-pipe traps were arranged in a matrix design spread evenly across the field site. The matrix consisted of 36 stand-pipe traps in twelve rows of three, spaced out at 7m intervals along the centre of the stream (Fig. 5). Within each row one stand-pipe trap was positioned at each different depth of 10 cm, 20 cm and 30 cm within the subsurface, between rows stand-pipe trap depth position alternated (see Fig. 5). Stand-pipe traps were placed no closer than 1 m to each other to avoid interference with one another.

Twelve Hess samples of the stream benthos were taken randomly, each from within a 2 m x 6 m grid 1 m upstream from, and parallel to each row of stand-pipe traps. Hess samples were taken by positioning the sampler so that it faced the flow of water with the collecting vessel at the downstream end floating in the current (see Fig. 4 b). The bottom of the sampler with a sharp metal cutting edge was pushed down into a fixed position within the substrate. This ensured the sampler was not moved during collecting or any substrate or organisms could enter the sample area from underneath once the Hess device was put in place and used. The benthos within the Hess sampler area was then agitated by hand for 240 s, the flow of water entering through the 42 μm mesh at the front of the sampler pushing substrate and organisms into the collecting device at the downstream end. It was not possible to predict or control for growth of lotic macrophytes into sampling areas over the twelve month study period. It was therefore decided to record the presence or absence of lotic macrophytes in samples and modify statistical analyses appropriately (see data analysis).

In total, 36 standpipe-trap samples were taken each month, twelve replicates at each depth, and 12 benthic Hess samples each month except in June 2004 where 7 samples were taken and July where 11 samples were taken due to logistical problems.

Sample Processing

Stand-pipe trap and Hess samples were kept cool during transport to the lab where they were refrigerated. Total volume of each sample collected from stand-pipe traps was then recorded. Each stand-pipe trap and Hess sample was separated into the macrofaunal (>500 μm) fraction, immediately preserved in ethanol for later sorting and counting, and meiofaunal (<500 μm) fraction which was kept refrigerated and sorted live.

Macrofauna

Counts and identification to the highest practicable taxonomic level, species where possible, were performed with a dissecting microscope Nikon SMZ-U (25-250x magnification), except for Chironomidae and Oligochaeta which were slide mounted with Euparal and identified using a high power compound microscope the Olympus BX50 (1250x magnification).

Meiofauna

Meiofauna fractions were sorted and counted live within one week of collection. Firstly, so that soft bodied taxa could be accounted for which are lost when sample preservation techniques are used, and secondly, because after one week meiofauna mortality rates in stored samples become too high to accurately represent densities of natural populations (Schmid-Araya, pers. comm.). Each sample was either fully searched or subsampled depending upon the volume of sediment or density of individuals found. Where

subsampling was required three and rarely five replicates achieved an acceptable sampling error of within 20% of sample population means following Elliot (1977). Subsampling was performed by diluting whole samples with distilled ultra pure water, and then re-suspending them in conical flasks, before removing smaller samples volumes containing meiofauna and sediment with a pipette.

Meiofauna were removed from sediments using a fine pipette and a dissecting microscope Nikon SMZ-U. Hard bodied meiofauna were preserved in a formalin solution (Nematoda) or 100% ethanol (all other hard-bodied taxa), and then identified and sorted. Chironomidae and Oligochaeta were identified after slide mounting with Euparal. Soft-bodied meiofauna such as Rotifera, Gastrotricha and Microturbellaria, were filmed using an Olympus BX50 (Olympus Optical, Tokyo, Japan) microscope connected to a 3CCD JVC video camera (JVC, Tokyo, Japan), and later identified usually to species and/or species types. A list of reference materials used for taxonomic identification of groups can be found in the appendix (Appendix 1).

Biomass Calculations

Measurements of body length and width to the nearest micrometer were taken for benthic invertebrates from samples collected within gravel beds and macrophyte stands. All invertebrates that occurred at low abundance within samples (<30 individuals found in all samples from a substrate type in one month) were measured. Abundant specimens (>30 individuals found in all samples from a substrate type in one month) were randomly subsampled until a size frequency distribution approximating a 10% sampling error of the mean was achieved. In total 6,131 individual measurements of body size were taken. Measurements were then converted to dry mass using published body length and biovolume

regressions assuming a specific density of 1.1, and a wet weight to dry weight conversion factor of 0.25 following Reiss (2006) (see Appendix 2).

Data analysis

Repeated measures ANOVA (rmANOVA) was used to test for differences in the amount of organic matter between macrophyte stands and gravel beds over sampling dates. OLS linear regression was used to describe the relationship between temperature and depth in the riverbed in January 2005.

Density and biomass data were log (x + 1) transformed to fit normal distributions before analysis with Statistica (Statsoft Inc. USA). rmANOVA was used to test for the individual and interaction effects of depth and season on densities of macrofauna, meiofauna, and dominant meiofaunal groups from the standpipe samples. General linear modelling (GLM) was used to compare densities of macrofauna with meiofauna on each sampling occasion within each depth layer.

Because seasonal growth and recession of macrophyte stands throughout the study period was unpredictable and resulted in uneven sampling of the benthic habitats each month. Monthly Hess samples from the different habitats were pooled into four seasons: spring (gravel, $n = 20$; macrophyte, $n = 16$), summer (gravel, $n = 12$; macrophyte, $n = 18$), autumn (gravel, $n = 21$; macrophyte, $n = 15$) and winter (gravel, $n = 21$; macrophyte, $n = 15$). rmANOVAs testing for the effects of habitat, season and combined, on density and biomass of the macrofauna, meiofauna, and dominant groups were then performed. GLM was used to investigate the interaction of total density and biomass of macrofauna and meiofauna between habitat types and seasons.

Annual and seasonal species rank-percentage abundance distributions between the two benthic habitats were tested using the non parametric Kolmogorov-Smirnov two

sample test. Species-abundance data were then arranged into $\log_2$ octaves according to mean body mass following Preston (1980) and a Kolmogorov-Smirnov normal distribution test applied. The statistical method provides an indication of whether species assemblages are derived from relatively stable or unstable environments based on the assumption that some species populations respond faster to environmental perturbations. They would therefore dominate unstable environments resulting in non-normal distributions.

RESULTS

Abiotic variables

The River Lambourn is a typical chalk river, circumneutral and relatively warm in the spring/summer and cooler in the autumn/winter, with a constant and high conductivity (Fig. 6). A marked reduction in discharge was observed between June 2004 and July 2004 when the Environment Agency adjusted a weir approximately 50 m upstream of the field site to reduce water flow in the stream channel (Fig. 6). Vertical hydraulic gradient (VHG) data showed a strong pattern of positive values dominating the whole field site in all months (Fig. 7a). In August 2004 the warmest month when measurements were taken, no noticeable pattern of temperature variation was observed between the surface and the subsurface which suggests that water mixing occurred (Fig. 7b). In contrast, during January 2005 when the coldest surface water temperature was recorded, a linear increase with increasing depth was found suggesting less mixing between surface and subsurface water ($F = 42.236$; $df = 1,39$; $P < 0.000$; Fig. 7b).

The percentage of organic matter marginally differed between the macrophyte stands and gravel beds but not sampling dates (rmANOVA; habitat = $F_{1,2}$ 6.946, $P < 0.077$; Sampling date = $F_{1,5}$ 0.477, $P < 0.787$; Fig. 8a). Whilst in the subsurface, the percentage of

organic matter was low in all depth layers and seasons; a peak mean value of 3.44% was observed n July 2005, however no obvious distributional patterns were found (Fig. 8b).

Hyporheic invertebrate densities

In total 57 metazoan species were identified from the hyporheic samples taken in the river Lambourn between April 2004 and March 2005 (Appendix 3). Overall, a pattern of decreasing density with increasing depth was found for both macro- and meiofauna on all sampling dates (Fig. 9). However the effect of sediment depth was only significant for the meiofauna (Table 1). Furthermore, meiofauna occurred at significantly higher densities than macrofauna in all depth layers and on all sampling occasion (Table 2, Fig. 9; all GLMs $P < 0.05$; except 20 cm April, March and 30cm February).

The three most dominant meiofaunal groups: Cyclopoida, Harpacticoida, and Nematoda contributed respectively 9%, 34% and 24% of the total meiofauna density, and showed the same pattern of depth distribution as the total meiofauna (see Fig. 9). However, significant depth effects were only found for Harpacticoida, and for the Nematoda there was a significant date x depth interaction (Table 1).

Surface invertebrate densities

In contrast to the subsurface, a total of 185 metazoan species were identified from benthic samples (Appendix 3). Densities of macro- and meiofauna within the macrophyte stands significantly exceeded those within gravel beds in all seasons (Table 3), despite similar macrofauna densities for both habitats during September 2004 and February 2005 (Fig. 10). Significant seasonal changes in the densities of both macro- and meiofauna were recorded between sampling dates with higher monthly mean densities found in macrophyte stands during the summer. The highest density peak of 19,653 ind. m^{-2} for macrofauna was

observed in August 2004, and of 126,000 ind. m^{-2} for the meiofauna in June 2004 (Fig. 10). Meiofauna were significantly more numerous than macrofauna on all sampling dates within both habitat types (Table 2; All GLMs $P < 0.01$; except July 2004 gravel bed and macrophyte stand densities $P < 0.05$).

Four taxonomic groups contributed most of the total macrofaunal density within at least one habitat type (Table 4). Within the gravel beds these taxa were: *Gammarus pulex* L. (Amphipoda), *Potamopyrgus antipodarum* (Gray) (Gastropoda), and *Agapetus fuscipes* Curtis (Trichoptera), contributing respectively to 48.6%, 14.1%, and 14.2% of the total density. In the macrophyte stands, *G. pulex*, *P. antipodarum* and *Simulium* spp. (Diptera) contributed to 47.7%, 14.3%, and 15.7% respectively of the total density. These taxa showed significant differences in density either between habitat types, seasons, or both except for *A. fuscipes* (see Table 3). Significantly higher densities of *G. pulex* and *Simulium* spp. occurred within the macrophyte stands on most sampling occasions (Fig. 11). It seems that the density pattern of *G. pulex* closely reflected that of the total macrofauna (Figs. 10 and 11), while *Simulium* spp. had two density peaks one in summer 2004 and another in autumn 2005 (Fig. 11). Densities of *P. antipodarum* followed a similar pattern in both habitats with peak values in the summer months and October 2004 (Fig. 11).

Within the meiofaunal size class, four taxonomic groups contributed greater than 70% of the total benthic density of gravel beds and macrophyte stands: Harpacticoida, Chironomidae, Nematoda and Oligochaeta (Table 3). Only Nematoda showed significantly higher densities in the macrophyte stands, whilst Harpacticoida displayed strong seasonal changes in density with an obvious peak in June 2004 (Table 3, Fig. 12). A weak seasonal change in density of Oligochaeta was found with a clear peak in September 2004, whilst a weak season, and season x habitat effect, was found for Chironomidae which showed higher densities in macrophyte stands in summer months (Fig. 12).

Surface invertebrate biomass

Macrofaunal biomass followed a similar pattern to that described for density with a significant effect of habitat type (Table 5). Macrofaunal biomass showed no effect of season however there was a significant habitat x season effect (Table 5) with highest values occurring in the macrophyte stands during the summer of 2004 (Fig. 13). Biomass of meiofauna showed significant effects of habitat type and season remaining high within macrophyte stands from the summer through the autumn despite no comparable pattern in density (Table 5, Figs. 13 &14).

Macrofauna dominated the biomass in both habitat types and on all sampling occasions in this chalk stream (Table 2; All GLMs $P < 0.01$; except for April 2004 macrophyte stand biomass $P < 0.05$). *G. pulex* contributed to most of the total biomass in both habitats: 32.2% in gravel beds and 51.7% in macrophyte stands. A second species *P. antipodarum* contributed to a further 10.6% and 16.4% in gravel beds and macrophyte stands respectively. These were the only taxa that exhibited significant variation with season and habitat type (Tables 4 and 5, Fig. 14). In both taxa the pattern of distribution for biomass closely resembled the pattern for total macrofauna biomass (see Fig. 14).

Nearly two thirds (63.4%) of the total meiofaunal biomass was dominated by only four taxa: Diptera: Chironomidae, meiofaunal size Gastropoda, Nematoda, and Oligochaeta in the gravel beds (Table 5). Within the macrophytes, the same four taxa along with other Diptera contributed to more than 85% of the total meiofaunal biomass (Table 4). Significantly higher biomass values were found for all meiofaunal groups except small gastropods in the macrophyte stands (Table 5, Fig. 15). Chironomidae and small gastropods exhibited significant changes in biomass with season (Table 5). Biomass peaks were observed in June, August and October for Gastropoda, and for Chironomidae in macrophyte stands during summer, and gravel beds in autumn-winter (Table 5, Fig. 15).

Nematodes showed a significant combined habitat x season effect with higher biomass in summer and autumn-winter within macrophyte stands (Fig. 15).

Species richness and area relationships

Within macrophyte stands species richness varied from 84 to 111 species during spring and summer respectively, in contrast to 80 and 62 species in the autumn and winter. Whereas in the gravel beds species richness only varied from 63 to 82 species in the spring and summer to 59 and 71 species in the autumn and winter. This pattern resulted in a more even spread of abundance amongst the gravel bed invertebrate assemblages (Fig. 16a). The Kolmogorov-Smirnov two sample tests revealed significant differences between the two benthic habitats in the distributions of species rank-abundance plots in the spring (macrophyte mean, 1.25 ± 0.38 S.E.; gravel mean, 1.58 ± 0.44 S.E.; $P < 0.05$), summer (macrophyte mean, 1.06 ± 0.45 S.E.; gravel mean, 1.21 ± 0.41 S.E.; $P < 0.001$), and also annually (macrophyte mean, 0.61 ± 0.23 S.E.; gravel mean, 0.73 ± 0.23 S.E.; $P < 0.001$). Temporal fluctuations in equitability probably reflected the seasonal changes in species richness. Despite temporal changes in equitability all $\log_2$ transformed species-abundance distributions were normally distributed (Fig. 16b, Kolmogorov-Smirnov; $D > 0.19$; P values > 0.05).

DISCUSSION

In the chalk stream the River Lambourn significantly higher densities of meiofauna mainly Nematoda, Harpacticoida and Chironomidae were found. However, biomass was dominated by the macrofauna, especially by the presence of *G. pulex* and to a lesser extent *Potamopyrgus antipodarum*. Macrophyte stands appear to be a more important habitat than gravel beds in supporting a higher species richness, density and biomass of invertebrates.

Over three times as many species were recorded from the benthos than the hyporheos. Overall for both macro- and meiofauna depth distribution was nearly completely restricted to the first 10 cm.

Hyporheic invertebrate densities

Comparisons of hyporheic invertebrate densities between studies are confounded by the variety of different sampling techniques used. There have been two reported studies by Schmid-Araya (1997) and Stead *et al.* (2004) which have used comparable stand-pipe trap sampling methods to this study. Schmid-Araya (1997) reported an increase in invertebrate densities to approximately 600 individuals per litre at 30-40 cm within a calcareous gravel stream, while Stead *et al.* (2004) found highest density values of 500 individuals per litre at a depth of 15 cm only in one sampling occasion. Consequently, the annual meiofaunal mean density of 185 individuals per litre (±SE 24) for the River Lambourn closely resembles the densities of Stead *et al.* (2004) recorded for an oligotrophic acidic stream.

The drastic significant reduction in density with depth of both macrofauna and meiofauna found within the river Lambourn contrast with the findings of Schmid-Araya (1997) and Stead *et al.* (2004), however similar patterns of decreasing density with depth have been reported from a sandy stream (Strommer & Smock, 1989) and a Canadian gravel stream (Franken *et al.* 2001). The invertebrate depth distribution in the River Lambourn might be related to a significant decrease in biogeochemical activity at depths in excess of 20 cm demonstrated by Pretty *et al.* (2006). Pretty *et al.* (2006) showed that there was a low connectivity of surface and subsurface water below that depth. The data presented here at least for the winter season when a steep temperature gradient occurred would seem to confirm this pattern. Furthermore, Pretty *et al.* (2006), speculated that the limited depth of the hyporheic zone could be a result of high positive pressure gradients evidenced by VHG

measurements in their study and this one, or an impermeable or low permeability barrier within the River Lambourn.

It seems unlikely that positive pressure gradients would restrict the depth distribution of the dominant meiofaunal groups found within the River Lambourn since they can all actively disperse. Moreover, all three groups have been found with significant densities at deeper depths than 30 cm within hyporheic zones (Dole-Olivier *et al.* 1997; Schmid-Araya, 1997), and also deeper than 20 cm within upwelling zones which are typically characterised by higher positive pressure gradients (Franken *et al.* 2001). We can also confidently rule out the impermeable barrier caused by a natural geologic feature such as for example the bedrock (Jones, 2002) as the cause of a shallow hyporheic zone. If the River Lambourn had shallow bedrock it would have been impossible to install standpipe traps to a depth of 20 or 30 cm. This is because there is a 20 cm distance to the base of each standpipe from the catching holes. Combined with the depth of the holes a minimum streambed sediment depth of 40 to 50 cm is required.

It is possible that an impermeable or low permeability layer may arise through precipitation of Fe and Mn into a solidified horizon (Cleven & Meyer, 2003), or colmation where fine sediments accumulate in the interstices of coarser substrata clogging pore spaces (Schälchli, 1992; Brunke, 1999). A gradual reduction in interstitial spaces would occur within the hyporheic zone between shallower more unstable depth layers to more stable and compact deeper layers where the influence of compound precipitation or colmation was greatest. Reduction in interstitial spaces can place severe restrictions on the hyporheic fauna (Hakenkamp & Palmer, 2000) which would then explain the reduction in meiofauna density with depth observed in the River Lambourn. Furthermore, macrofauna due to their size would be more limited than meiofauna, explaining their significantly lower densities within the hyporheic zone.

Synchronicity of meiofauna and macrofauna patterns

Due to differences in size meio- and macrofauna have different dispersal capabilities (Finlay, 2002), possess different generation times, and consequently are assumed to respond at different rates to environmental variables (Townsend & Hildrew, 1994; Stead *et al.* 2003). Within the River Lambourn density and biomass of both macro- and meiofauna were significantly higher within macrophyte stands. Total density of both taxa showed remarkably similar seasonal patterns with peak values in summer months, but only in the macrophyte stands. The total biomass pattern for macrofauna resembled that of density. Despite a significant reduction in density after the summer, high monthly mean biomass values were sustained for meiofauna well into the autumn.

Higher densities of benthic macroinvertebrates within lotic macrophyte stands are well documented (Wright & Symes, 1999; Harrison *et al.* 2005), but higher meiofauna densities within higher plant macrophyte stands have only been reported from lentic habitats (Paterson, 1993; Silver & Cowell, 1993). Meiofaunal densities were between 1.3 and 5.4 times greater, and biomass between 1.1 and 4.7 times greater, in macrophyte stands than in gravel beds in the River Lambourn. In lentic macrophyte habitats, meiofauna and their food sources such as bacteria, fungi, and algae are thought to benefit from an increase in habitable surface area, refugia from physical conditions, and/or predation through presence of macrophytes (Carpenter & Lodge, 1986; Brown *et al.* 1988). Lotic macrophytes are known to increase benthic habitat complexity directly through growth, and indirectly through modification of flow resulting in increased deposition of sediment, which also creates patches of concentrated organic matter (White & Hendricks, 2000). Organic matter concentrations were only marginally higher within macrophyte stands than gravel beds in the River Lambourn. However meiofaunal distributions are known to be strongly linked to the presence of organic matter (Palmer *et al.* 2000; Silver *et al.* 2002). Organic

matter not only provides an important food source for meiofauna, but also structure as colonisable habitat (Swan and Palmer, 2000).

The spatial distribution patterns of higher total density and biomass of macrofauna and meiofauna in macrophyte stands within the River Lambourn probably reflect the 'better' habitat quality when compared to bare gravel beds. In addition, the higher densities of both macrofauna and meiofauna in the macrophyte stands during summer probably reflect the enhancement of the habitat caused by new plant growth which occurs at this time (Ham *et al.* 1982).

Comparisons of invertebrate density and biomass

The values for benthic density of meiofauna with maxima of 126,000 ind. m^{-2} in macrophyte stands and 39,000 ind. m^{-2} in gravel beds, are comparable with studies of lotic benthic populations by Bott and Borchardt (1999; 443,000± 343,000 ind. m^{-2}), and Stead *et al.* (2003; 100,000 ind. m^{-2}). Whilst the biomass estimates with maxima of around 455,400 $\mu g\ m^{-2}$ for macrophyte stands and 222,400 $\mu g\ m^{-2}$ for gravel beds are consistent with values obtained from other streams and rivers (Poff *et al.* 1993; Ramsay *et al.* 1997).

Within marine systems meiofauna can be between 30 and 190 times more abundant than macrofauna (McIntyre, 1969; Giere, 1993). Stead *et al.* (2003) found meiofauna 2 to 22 times more abundant than macrofauna. Meiofauna were between 4 and 17 times more abundant than macrofauna in the River Lambourn.

Stead *et al.* (2003) only found significant differences in invertebrate biomass on one sampling occasion. Within the River Lambourn a significantly higher biomass of macrofauna was found on all sampling occasions in both habitat types. In the few published studies investigating meiofauna biomass, percentage contributions to total invertebrate biomass range between 0.01% up to only 22% (Hakenkamp *et al.* 2002). The maximum

and minimum recorded values for contribution of meiofauna within the river Lambourn fell within the range of literature values at between 0.74% and 8.72%.

Generally there was a lack of correspondence between the macro- and the meiofauna in terms of density and biomass. This may be due to less dominance by single taxa in the meiofauna community, and the ability of meiofauna species to have multiple generations all year round particularly in the Harpacticoida and Nematoda (Galassi *et al.* 2002; Traunspurger, 2002) which enable constant new contributions to total meiofauna biomass.

Dominant invertebrate groups

Significantly higher densities of all dominant macrofauna taxa were found within macrophyte stands except for the trichopteran *A. fuscipes*, for which no clear seasonal patterns in abundance were found. The genus *Simulium* showed two peaks in abundance, one in late spring and another in late autumn, these results coincide with observations on their bi- or multivoltinism (Waters, 1977). The freshwater snail *P. antipodarum* showed seasonal peaks in abundance and biomass in both habitats that closely matched one another, notably with peaks in summer contributing substantially to the overall macrofauna seasonal density and biomass patterns. Changes in the density and biomass of *G. pulex* closely resembled patterns observed for total macrofauna. Moreover, the density and biomass estimates for *G. pulex* are comparable with those of Welton (1979) for a different chalk stream.

The distribution of density and biomass in the macrofauna appears to be driven by the amphipod *G. pulex*, and to a lesser extent by the freshwater snail *P. antipodarum*. In contrast, the seasonal density and biomass pattern in the meiofauna appears to be more complicated. Despite a strong overall density distribution pattern for the meiofauna

seasonally and between habitats, only Nematoda displayed a strong effect of habitat type, and the Harpacticoida of season. A significantly higher biomass of nematodes, chironomids, and oligochaetes was found in the macrophyte stands. Nematoda showed a combined effect of habitat with season and peak biomass occurred during the summer months. For the chironomids, peak biomass occurred in the macrophyte stands during summer months probably synchronised with times of emergence for dominant species. However, secondary peaks in biomass occurred in gravel beds during the autumn. This is not surprising as Chironomidae species do not all synchronise emergence at the same time of year and a significant number of large predatory taxa were found in the autumn which may have disproportionately increased the biomass (S. Tod, Pers. obs.).

Species richness and abundance relationships

The difference in equitability, associated with differences in species richness, particularly the significant seasonal changes in spring and summer are probably due to the seasonal influx of insect taxa in the macrophyte stands. Most of the seasonal peak was probably due to species of Chironomidae (Diptera) for which over 60 species were identified, approximately one third of the total benthic species richness recorded from the River Lambourn in this study. Not only were they a highly speciose group, but they exhibited significantly higher densities in macrophyte stands in the meiofaunal size class during the summer, and they were only the third most abundant meiofaunal, and fourth most abundant macrofaunal group. The contribution of chironomids species during the spring and summer season might have significantly altered the equitability of abundance amongst the entire invertebrate assemblage.

Despite significant differences between the two habitats in spring, summer and annually all $\log_2$ abundance data were normally distributed. Log-normal distributions are

thought to be good descriptors of undisturbed areas so this may indicate a community in equilibrium (Schmid, 1992). This is because species would recolonise an area such as a streambed subjected to a spate at different rates from one another resulting in uneven distributions of abundance within a community. The River Lambourn is a typical chalk stream with rather stable discharge and a rural catchment, thus a log-normal distribution of species-abundance might have been expected as major perturbations of the site are probably rare.

Conclusions

The hyporheic zone appears to be of limited importance to lotic invertebrates within the chalk stream River Lambourn. Even meiofauna which are especially well suited to inhabiting interstitial spaces due to their small size were more or less absent below a depth of 20 cm, beyond which Pretty *et al.* (2006) found that biological activity decreased rapidly. Moreover, in another chalk stream Bird (1982) also found low oligochaete hyporheic densities, which strengthens the argument that the hyporheic zones is of extremely limited importance in chalk dominated lotic environments. However, it is now apparent that lotic macrophytes not only form one of the most important habitats in terms of densities, biomass and species richness for macroinvertebrates, but can also as this study shows for the first time do the same for meiofauna in chalk streams. What is more remarkable is that there is an apparent synchronicity in the seasonal response of densities of both size classes of stream invertebrate to growth of lotic macrophytes.

Table 1. rmANOVA results for the effect of sediment depth and sampling date on subsurface densities of macrofauna, meiofauna, and the dominant meiofaunal groups Cyclopoida, Harpacticoida and Nematoda. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Source of Variation	*df*	*MS*	*F*	*P*
Macrofauna				
Depth (D)	2	2.382	1.706	0.201
Sampling Date (S)	11	2.737	0.936	0.508
S x D	22	0.099	0.709	0.830
Meiofauna				
Depth (D)	2	30.221	7.115	0.003**
Sampling Date (S)	11	1.966	0.610	0.818
S x D	22	0.325	1.158	0.286
Cyclopoida				
Depth (D)	2	1.113	0.650	0.530
Sampling Date (S)	11	2.476	0.800	0.640
S x D	22	0.216	1.007	0.456
Harpacticoida				
Depth (D)	2	13.968	4.464	0.022*
Sampling Date (S)	11	5.482	1.846	0.052
S x D	22	0.402	1.288	0.178
Nematoda				
Depth (D)	2	7.406	2.513	0.101
Sampling Date (S)	11	1.147	0.352	0.972
S x D	22	0.325	1.641	0.037*

Table 2. General linear model results for the comparison of meiofauna and macrofauna density within the three stand-pipe trap sampling depths, two benthic habitats, as well as biomass of the size classes within the benthic habitats. (F statistics and *** P <0.001, ** P <0.01, * P <0.05, n.s. = no significance)

	Standpipe density ($\log_{10} x + 1$)			Benthic density ($\log_{10} x + 1$)		Benthic biomass ($\log_{10} x + 1$)	
	10 cm	20 cm	30 cm	Gravel	Macrophyte	Gravel	Macrophyte
23 Apr 04	18.191 ***	1.721 ^{ns}	6.620 **	160.584 ***	36.239 ***	66.557 ***	9.497 *
19 May 04	49.255 ***	22.124 ***	19.644 ***	47.886 ***	23.890 **	92.330 ***	131.440 ***
21 Jun 04	27.615 ***	17.735 ***	6.143 *	63.291 **	38.885 ***	151.741 ***	128.568 ***
19 Jul 04	40.948 ***	17.034 ***	6.928 *	11.367 *	7.023 *	61.805 **	185.646 ***
21 Aug 04	15.263 ***	29.629 ***	5.672 *	49.998 ***	14.363 **	71.891 ***	45.720 ***
25 Sep 04	12.585 **	15.911 ***	13.769 **	14.915 **	54.737 **	49.985 ***	25.489 **
22 Oct 04	24.872 ***	10.601 **	7.551 *	16.315 **	28.584 ***	37.339 ***	34.069 ***
20 Nov 04	18.625 ***	6.976 *	6.852 *	12.866 **	19.123 **	11.508 **	93.776 ***
20 Dec 04	15.565 ***	5.876 *	16.055 ***	63.151 ***	55.731 ***	72.670 ***	73.034 ***
22 Jan 05	11.727 **	9.117 **	13.081 **	50.868 ***	14.491 **	93.880 ***	33.173 ***
12 Feb 05	7.191 *	6.869 *	1.278 ^{ns}	32.302 ***	34.254 ***	67.950 ***	24.433 **
27 Mar 05	8.374 **	3.62 ^{ns}	12.373 **	51.151 ***	40.839 ***	88.086 ***	46.098 ***

Table 3. rmANOVA results for the effects of habitat type and season on benthic densities of macrofauna, meiofauna, and dominant invertebrate taxa. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

	Effects	df	*F*	*P*-level
Macrofauna	Habitat (H)	1,12	15.312	0.002**
	Season (S)	3,36	6.092	0.002**
	H x S	3,36	0.655	0.585
Gammarus pulex	Habitat (H)	1,12	6.384	0.027*
	Season (S)	3,36	9.210	0.000***
	H x S	3,36	5.534	0.003**
Agapetus fuscipes	Habitat (H)	1,12	0.626	0.444
	Season (S)	3,36	1.646	0.196
	H x S	3,36	0.713	0.551
Simulium spp.	Habitat (H)	1,12	46.485	0.000***
	Season (S)	3,36	3.586	0.023*
	H x S	3,36	0.310	0.818
Potamopyrgus antipodarum	Habitat (H)	1,12	3.131	0.102
	Season (S)	3,36	23.437	0.000***
	H x S	3,36	0.817	0.493
Meiofauna	Habitat (H)	1,12	12.962	0.004**
	Season (S)	3,36	3.592	0.023*
	H x S	3,36	2.587	0.068
Chironomidae	Habitat (H)	1,12	1.458	0.251
	Season (S)	3,36	2.641	0.064
	H x S	3,36	2.827	0.052
Harpacticoida	Habitat (H)	1,12	0.936	0.353
	Season (S)	3,36	5.563	0.003**
	H x S	3,36	0.266	0.849
Nematoda	Habitat (H)	1,12	6.183	0.029*
	Season (S)	3,36	1.473	0.238
	H x S	3,36	1.871	0.152
Oligochaeta	Habitat (H)	1,12	2.515	0.139
	Season (S)	3,36	2.670	0.062
	H x S	3,36	0.784	0.510

Table 4. Percentage of total abundance and biomass of macrofauna and meiofauna collected in modified Hess samples from gravel beds and macrophyte stands from April 2004 to March 2005.

	Gravel beds		Macrophyte stands	
	% Total Abundance	% Total Biomass	% Total Abundance	% Total Biomass
Macrofauna				
Coleoptera: Elmidae	0.6	0.4	1.1	0.6
Crustacea: *Gammarus pulex*	48.6	32.2	47.7	51.7
Other Crustacea	0.1<	0.1<	0.5	1.3
Diptera: Chironomidae	2.4	0.5	7.3	0.8
Diptera: Simuliidae	4.1	1.1	15.7	5.7
Diptera: Limoniinae	0.5	42.2	0.2	10.3
Other Diptera	2.3	0.1<	0.8	0.1<
Ephemeroptera	4.8	1.4	2.9	2.1
Gastropoda: *Potamopyrgus antipodarum*	14.1	10.6	14.3	16.4
Other Gastropoda	0.9	1.7	0.7	1.5
Hirudinea	0.1	0.4	0.2	0.6
Oligochaeta	6.2	2.3	3.0	1.7
Plecoptera	0.1<	0.1<	0.1<	0.1<
Trichoptera: *Agapetus fuscipes*	14.2	5.6	4.3	1.9
Other Trichoptera	1.0	1.7	1.0	5.3
Turbellaria	0.1<	0.1<	0.1<	0.1<
Meiofauna				
Acari	0.5	0.9	1.2	2.0
Microcrustacea: Harpacticoida	15.4	7.4	14.0	4.6
Other Microcrustacea	8.1	4.5	9.4	5.7
Diptera: Chironomidae	14.2	17.5	12.0	10.6
Other Diptera	2.0	6.4	4.0	13.4
Ephemeroptera	4.5	3.8	1.7	1.4
Gastropoda	7.5	10.3	8.3	11.9
Gastrotricha	0.6	0.1<	0.0	0.0
Microturbellaria	2.2	1.9	0.7	0.1
Nematoda	29.1	17.8	36.2	22.5
Oligochaeta	12.6	29.1	11.5	27.4
Plecoptera	0.1	0.1<	0.0	0.0
Rotifera	1.9	0.1<	0.5	0.03
Tardigrada	0.4	0.1<	0.4	0.02
Trichoptera	0.2	0.3	0.1	0.2
Turbellaria	0.1	0.1<	0.0	0.0

Table 5. rmANOVA results of the effect of habitat type and season on the biomass of macrofauna, meiofauna, and dominant invertebrate taxa. *** P <0.001, ** P <0.01, * P <0.05

	Effects	df	F	P-level
Macrofauna	Habitat (H)	1,13	8.382	0.013*
	Season (S)	3,36	2.550	0.070
	H x S	3,36	3.761	0.018*
Gammarus pulex	Habitat (H)	1,13	14.578	0.002**
	Season (S)	3,36	5.595	0.003**
	H x S	3,36	8.497	0.000***
Potamopyrgus antipodarum	Habitat (H)	1,13	4.665	0.050*
	Season (S)	3,36	20.213	0.000***
	H x S	3,36	4.826	0.006**
Limoniinae	Habitat (H)	1,13	0.085	0.776
	Season (S)	3,36	0.707	0.554
	H x S	3,36	1.381	0.263
Meiofauna	Habitat (H)	1,12	11.590	0.005**
	Season (S)	3,36	5.786	0.002**
	H x S	3,36	0.989	0.409
Chironomidae	Habitat (H)	1,12	5.186	0.042*
	Season (S)	3,36	3.519	0.025*
	H x S	3,36	2.096	0.118
Nematoda	Habitat	1,12	9.744	0.009**
	Season	3,36	2.579	0.069
	H x S	3,36	2.862	0.050*
Gastropoda	Habitat (H)	1,12	3.135	0.102
	Season (S)	3,36	5.142	0.005**
	H x S	3,36	0.160	0.923
Oligochaeta	Habitat (H)	1,12	6.629	0.024*
	Season (S)	3,36	2.516	0.074
	H x S	3,36	0.613	0.611

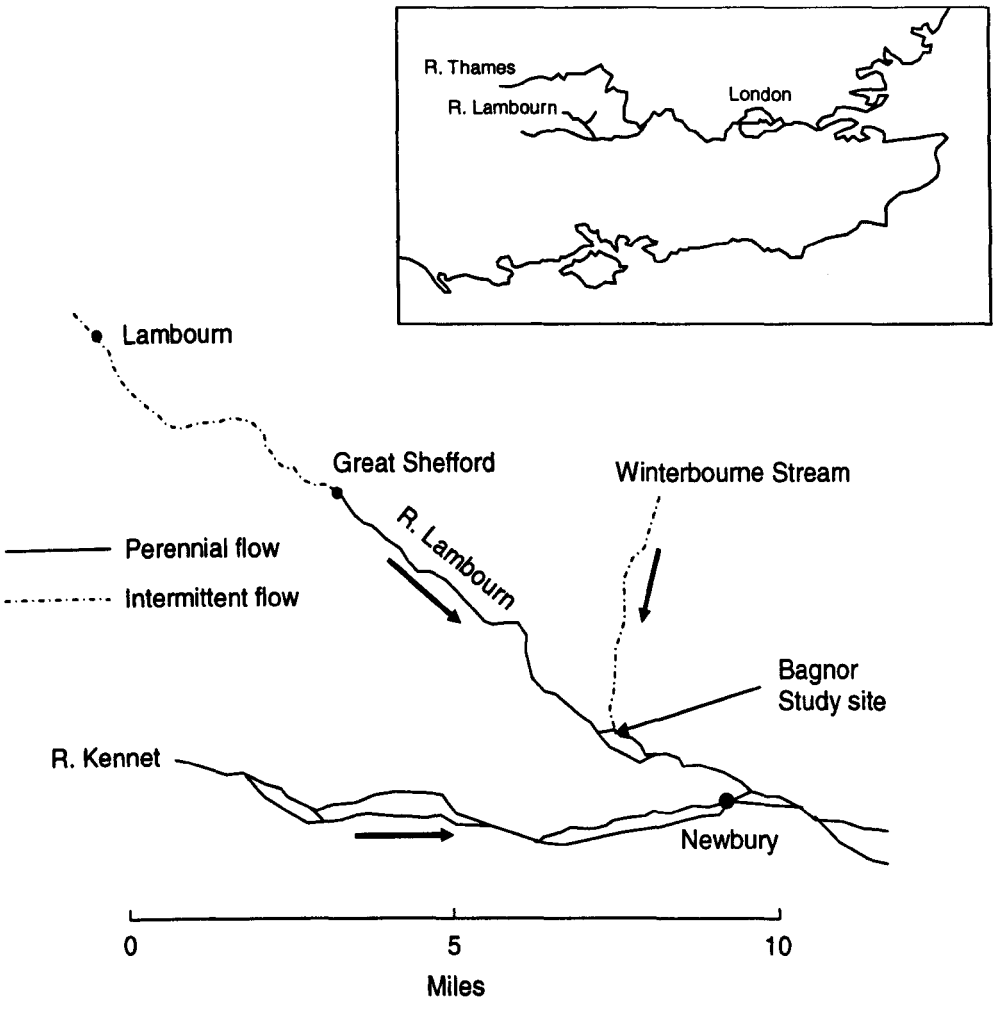

Figure 1. Map of the River Lambourn with the Bagnor study site indicated.

Figure 2. The field site at Bagnor before and after placement of sampling equipment.

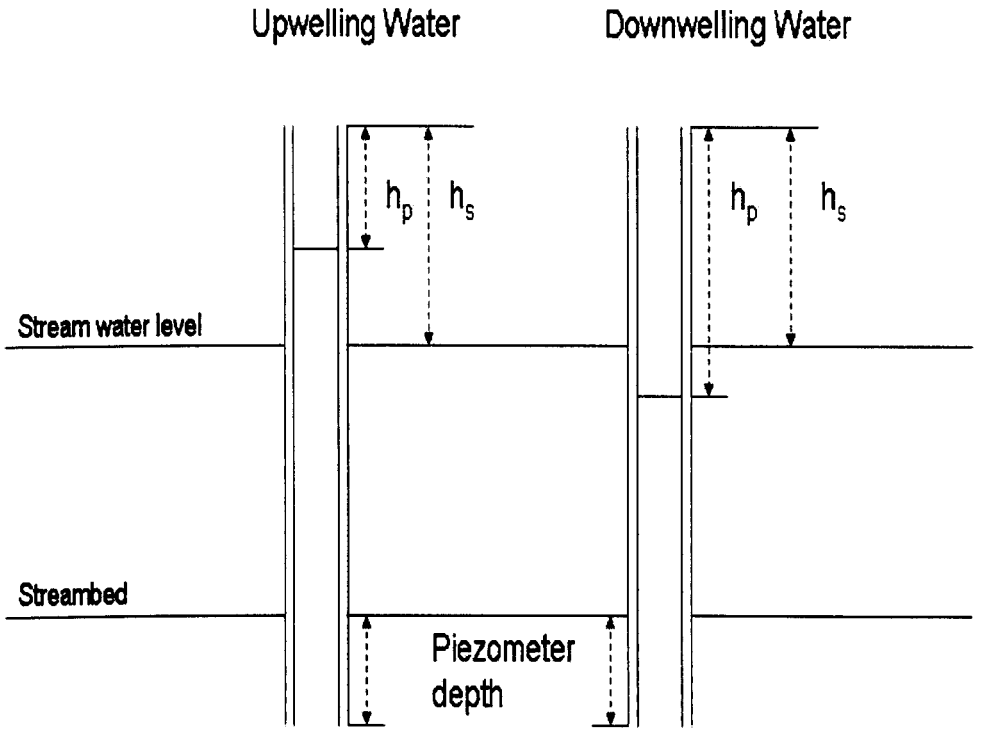

Figure 3. Schematic diagram of the Wagner and Bretschko (2003) mini-piezometer method, displaying the relative positions of stream water inside the piezometer, h_p, outside the piezometer, h_s, which characterise upwelling and downwelling hyporheic water movements.

Figure 4. Stand-pipe traps (a) used to sample the subsurface, and the modified Hess samples (b) used to sample the stream benthos of the River Lambourn.

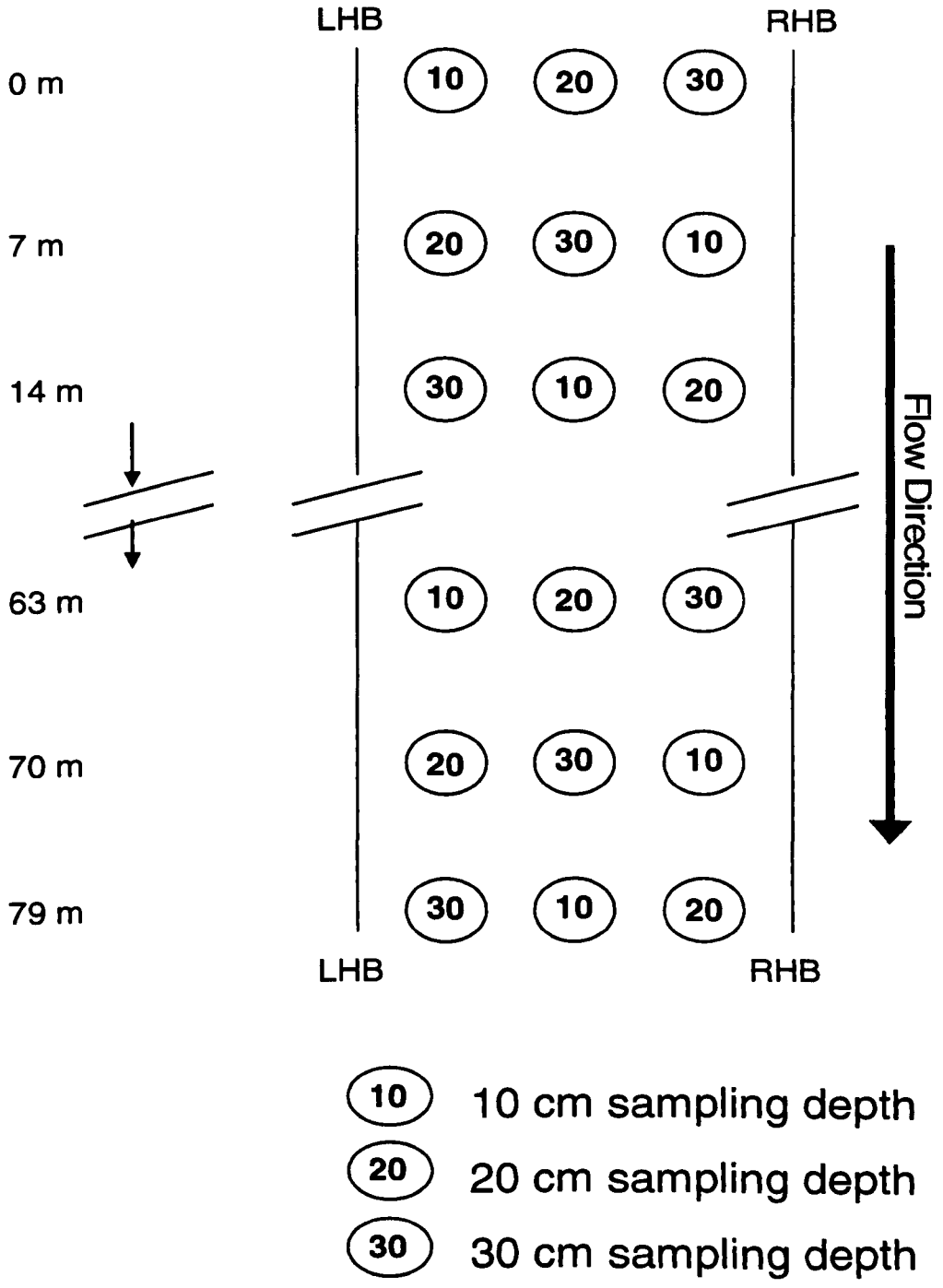

Figure 5. Schematic diagram showing the arrangement of the standpipe-traps within the field site used to sample the hyporheic zone of the River Lambourn between 2004 and 2005.

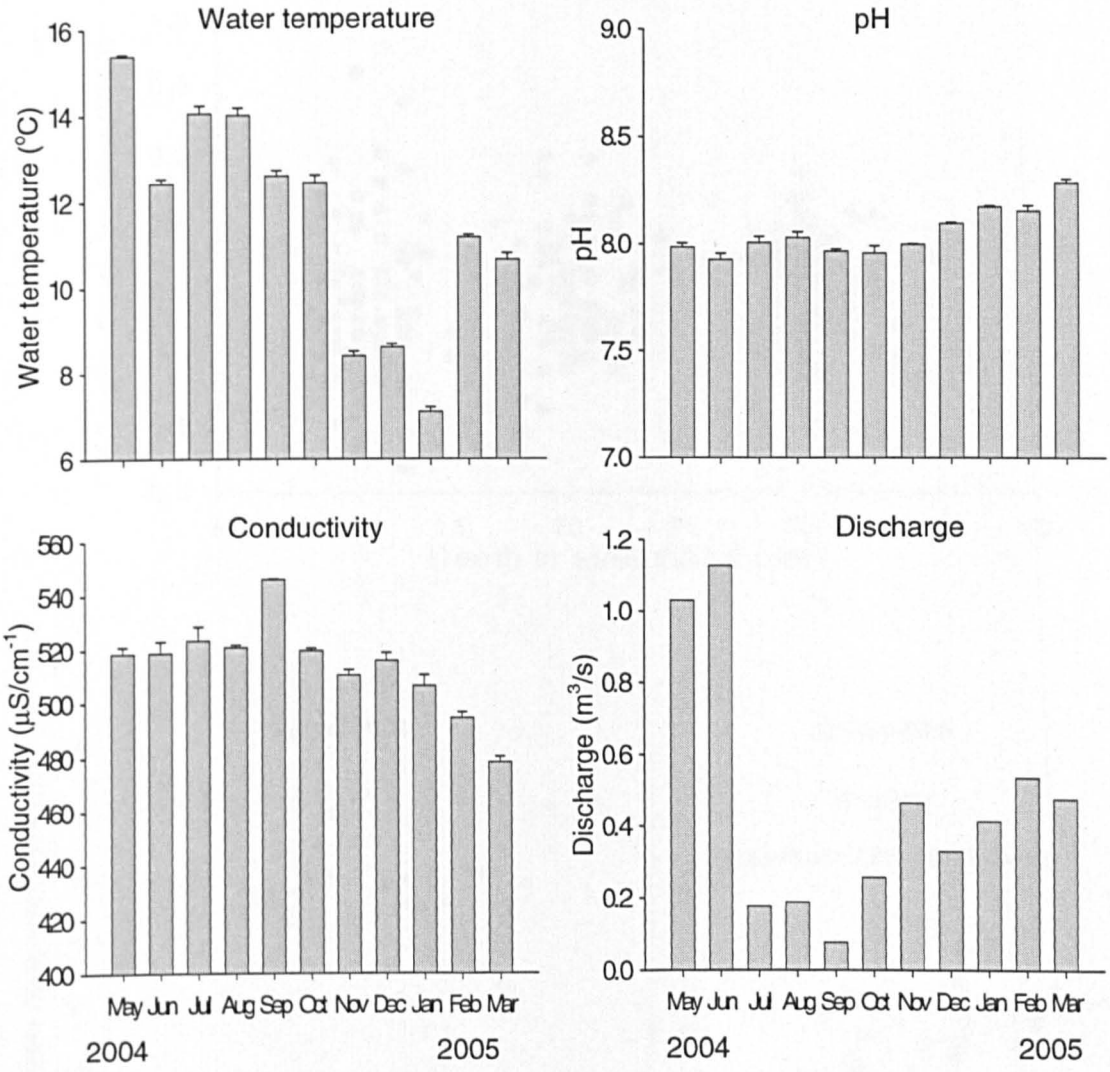

Figure 6. Monthly mean (±1SE) measurements of surface water temperature, pH, and conductivity, along with monthly discharge estimates for the River Lambourn at Bagnor from May 2004 to March 2005.

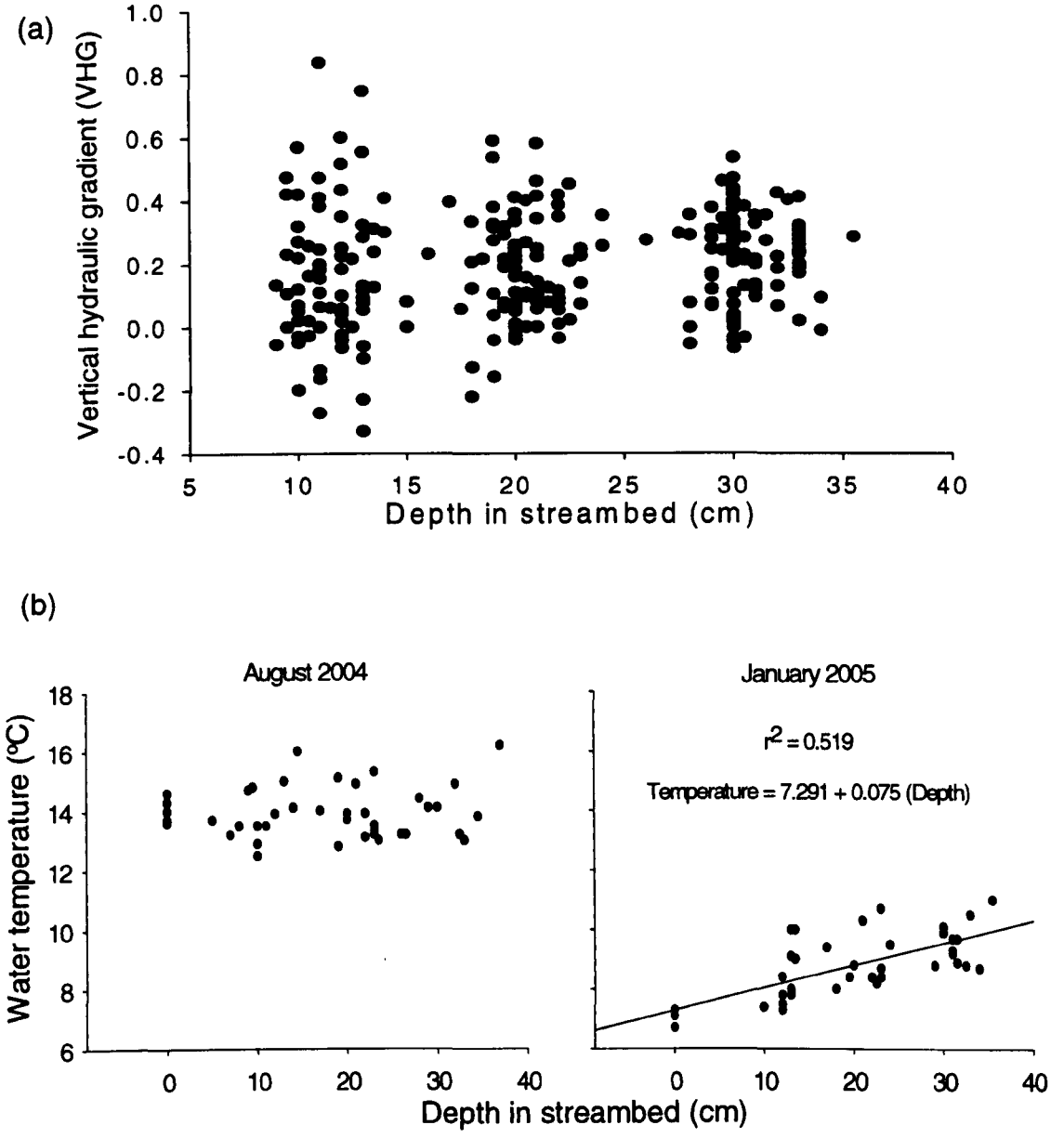

Figure 7. (a) Vertical hydraulic gradients measured at three depths: 10 cm, 20 cm, and 30 cm of the streambed from August 2004 until March 2005, and (b) temperature gradients within the streambed shown for two contrasting months in August 2004 and January 2005.

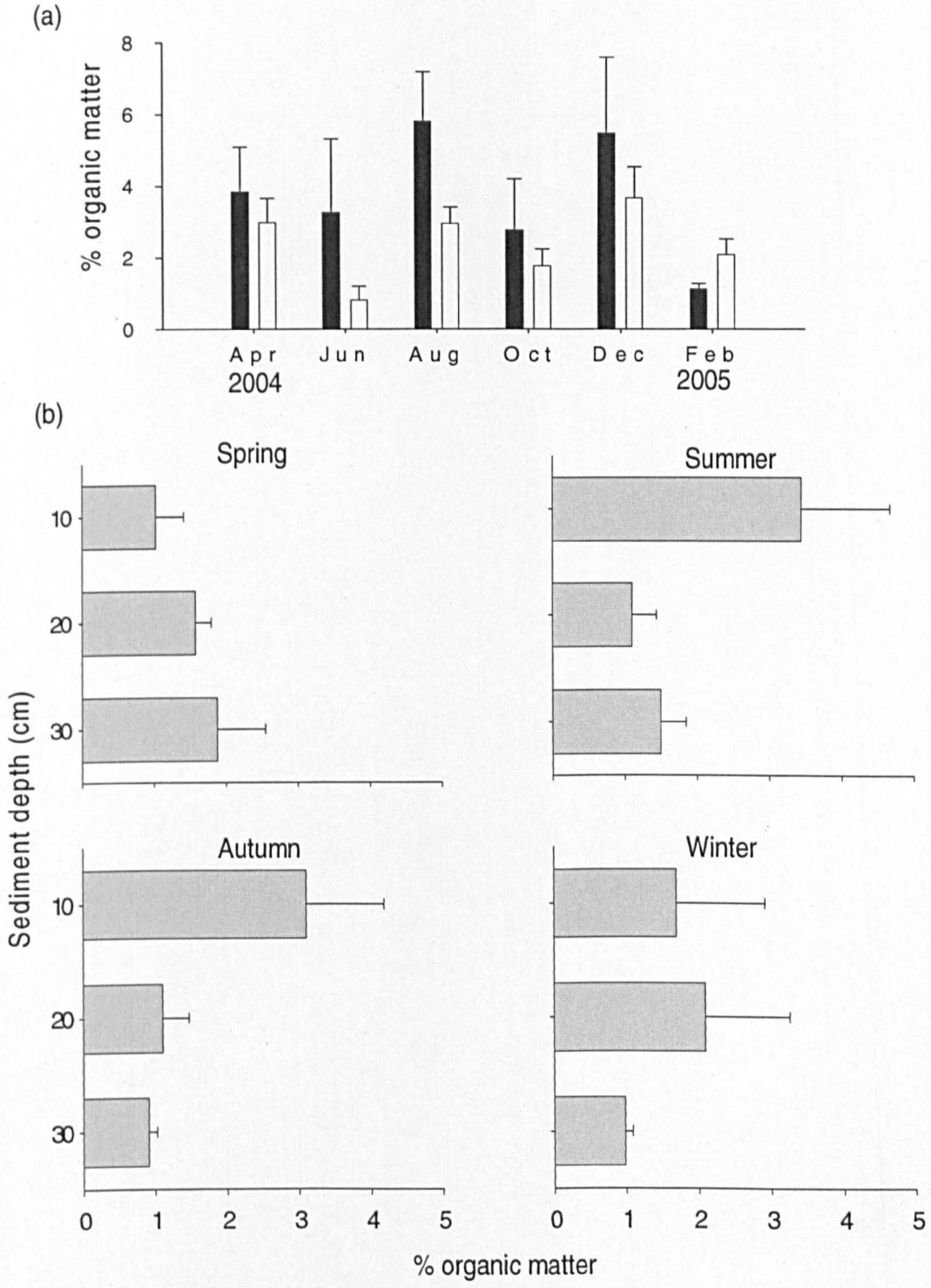

Figure 8. Percentage of organic matter (±SE) from (a) bimonthly benthic invertebrate samples of macrophyte stands (black bars) and gravel beds (white bars), and (b) seasonal stand-pipe trap samples of 10 cm, 20 cm, and 30 cm depths, taken from the River Lambourn during April 2004 to March 2005.

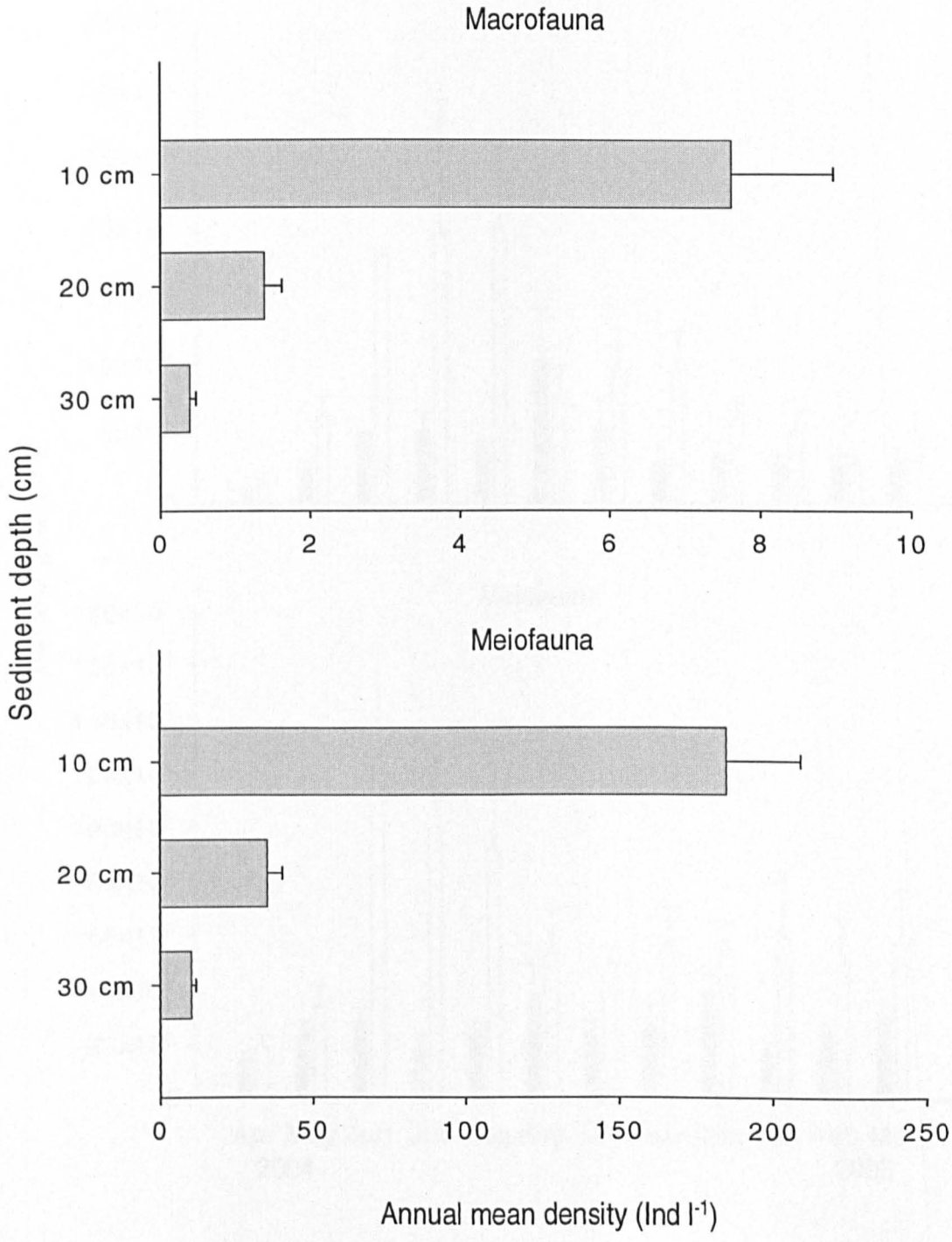

Figure 9. Annual mean density (±1SE) of macrofauna and meiofauna within the hyporheic zone (0-30 cm) of the River Lambourn between April 2004 and March 2005.

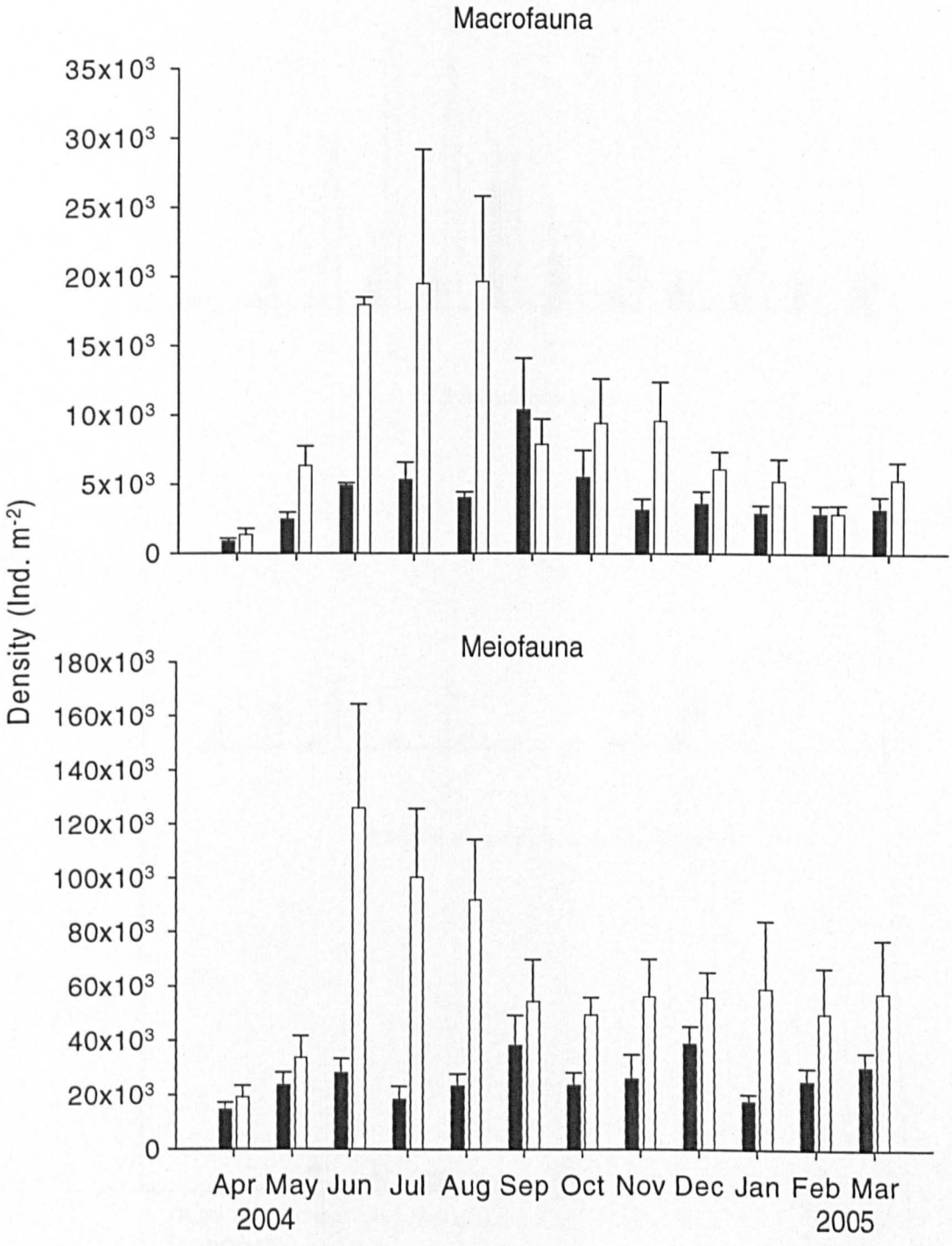

Figure 10. Monthly mean (±1 SE) density of macrofauna and meiofauna within gravel beds (black bars) and macrophyte stands (white bars) in the River Lambourn between April 2004 and March 2005.

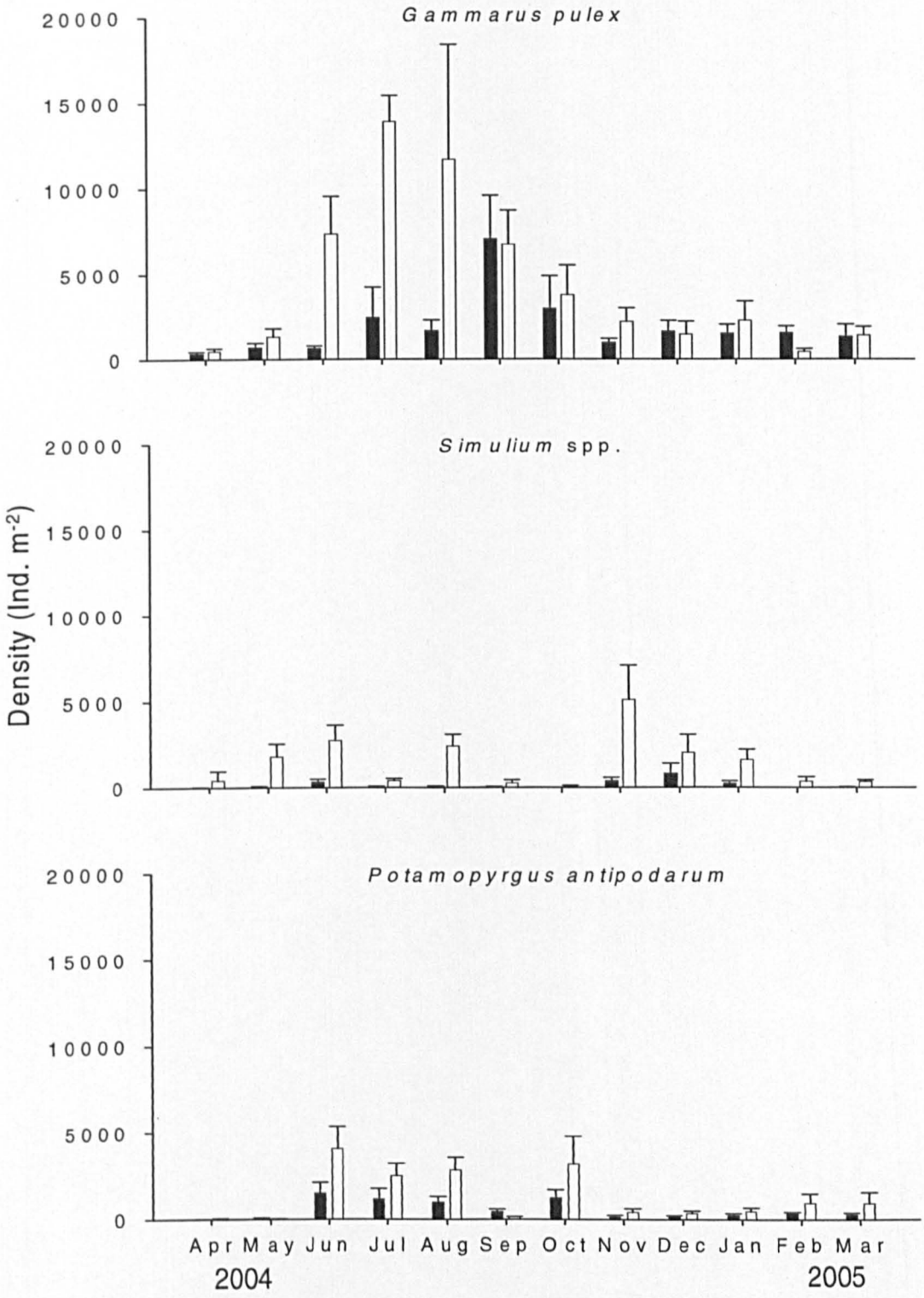

Figure 11. Monthly mean (±1 SE) density of the dominant macrofaunal groups; *Gammarus pulex*, *Simulium spp.* and *Potamopyrgus antipodarum*, within gravel beds (black bars) and macrophyte stands (white bars) of the River Lambourn between April 2004 and March 2005.

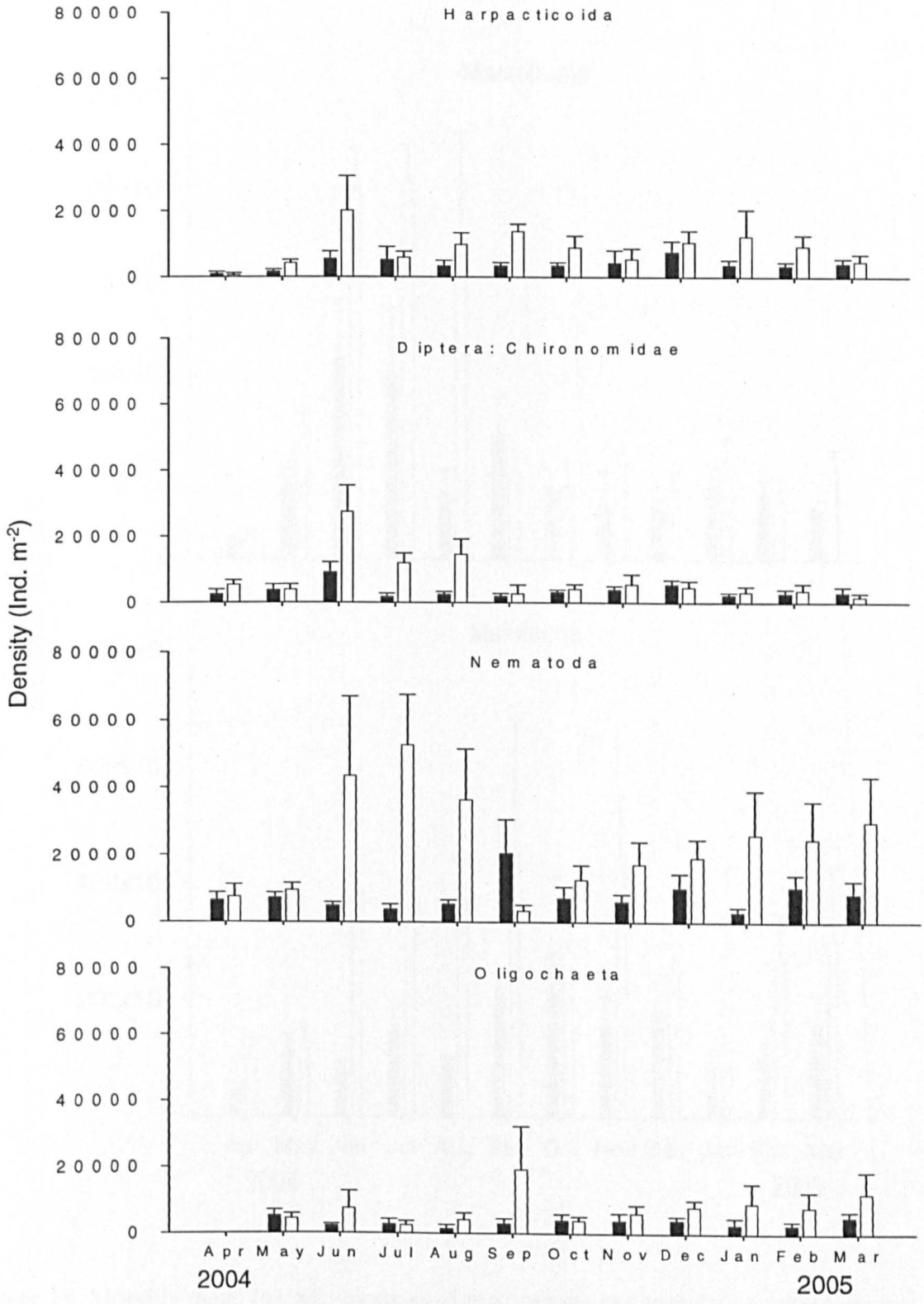

Figure 12. Monthly mean (±1 SE) density of the dominant meiofaunal groups; Harpacticoida, Diptera: Chironomidae, Nematoda, and Oligochaeta within gravel beds (black bars) and macrophyte stands (white bars) of the River Lambourn between April 2004 and March 2005.

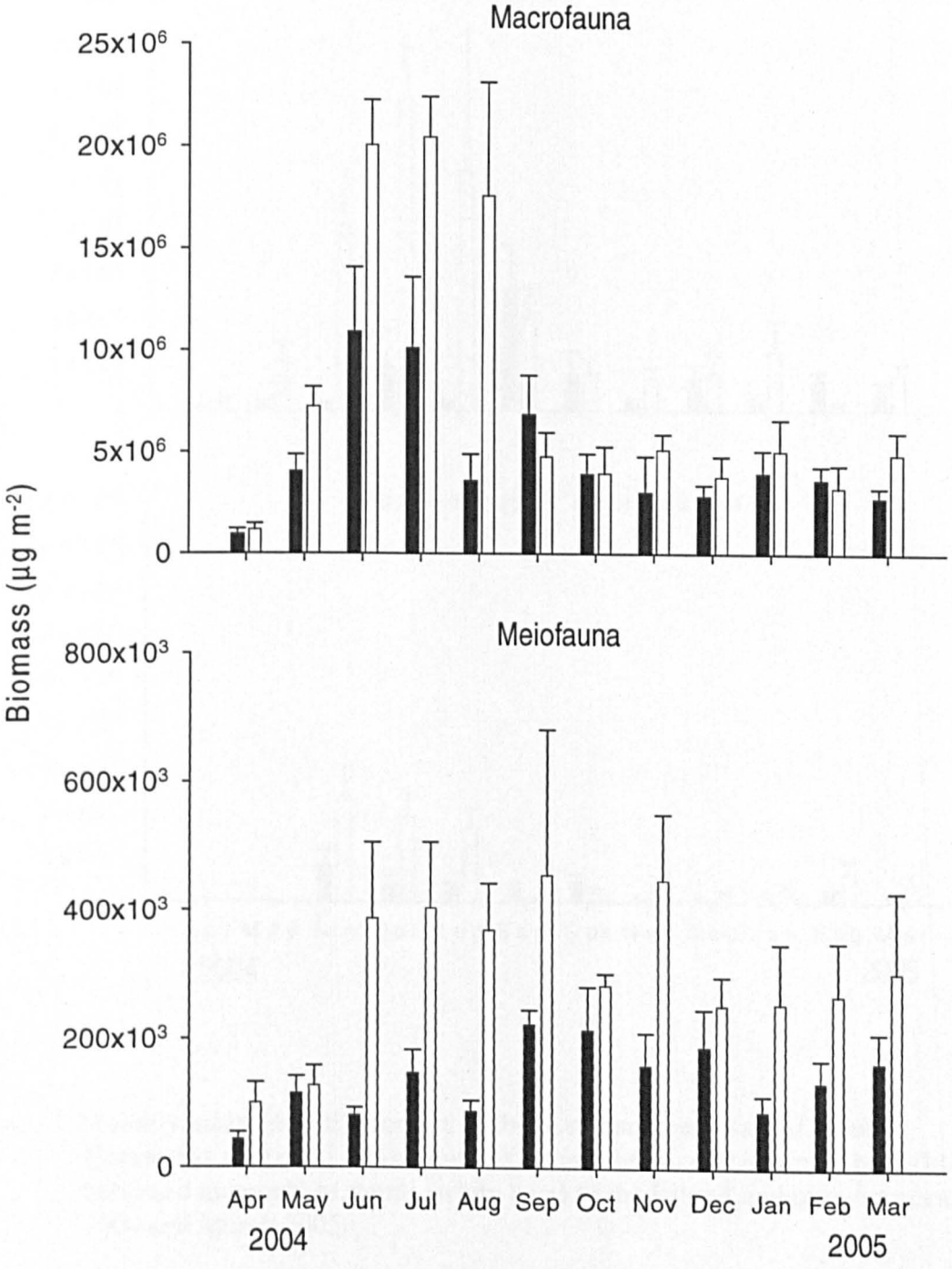

Figure 13. Monthly mean (±1 SE) biomass of macrofauna and meiofauna within gravel beds (black bars) and macrophyte stands (white) between April 2004 and March 2005.

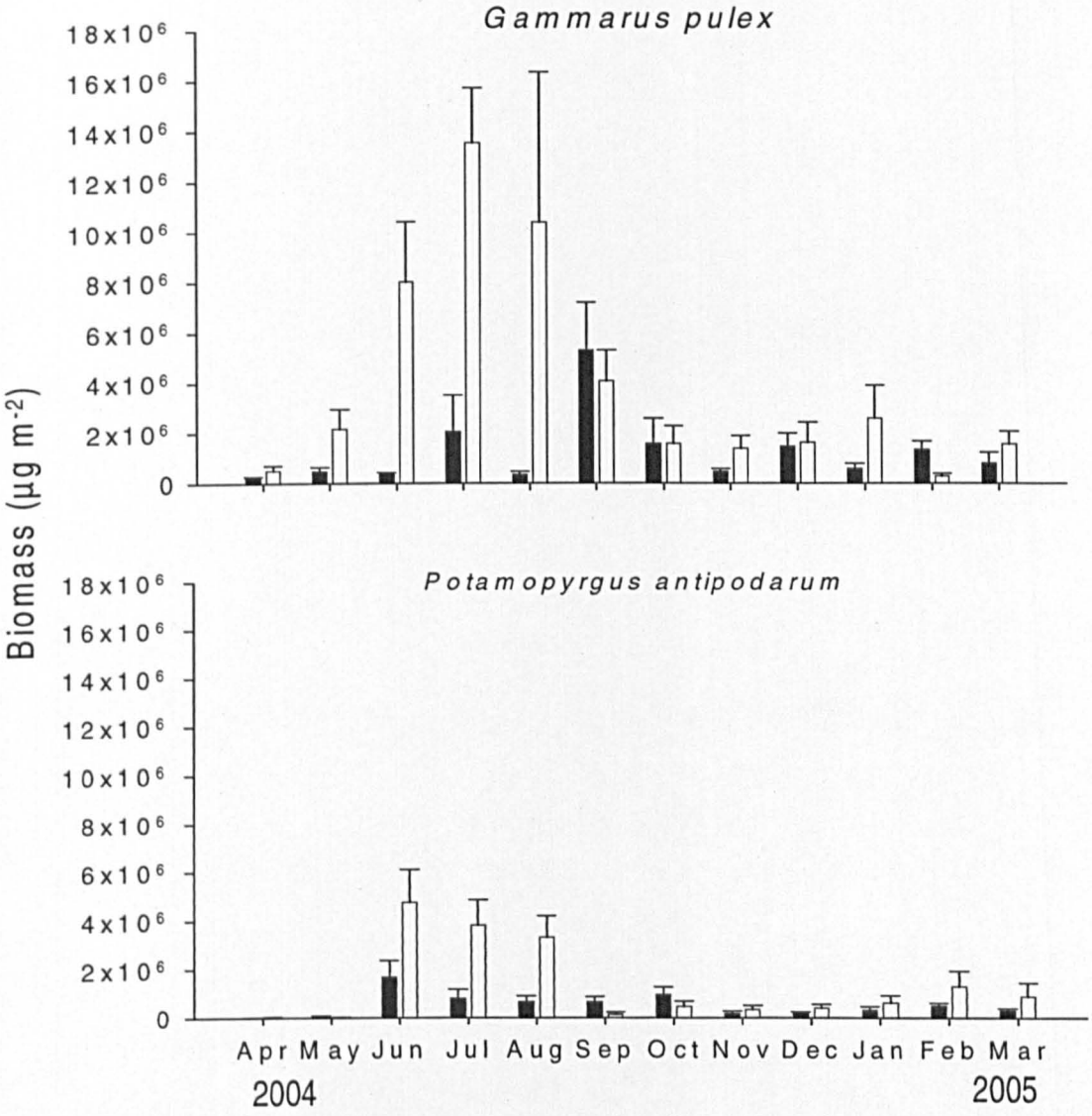

Figure 14. Monthly mean (±1 SE) biomass of the dominant macrofaunal groups; *Gammarus pulex* and *Potamopyrgus antipodarum*, within gravel beds (black bars) and macrophyte stands (white bars) of the River Lambourn between April 2004 and March 2005.

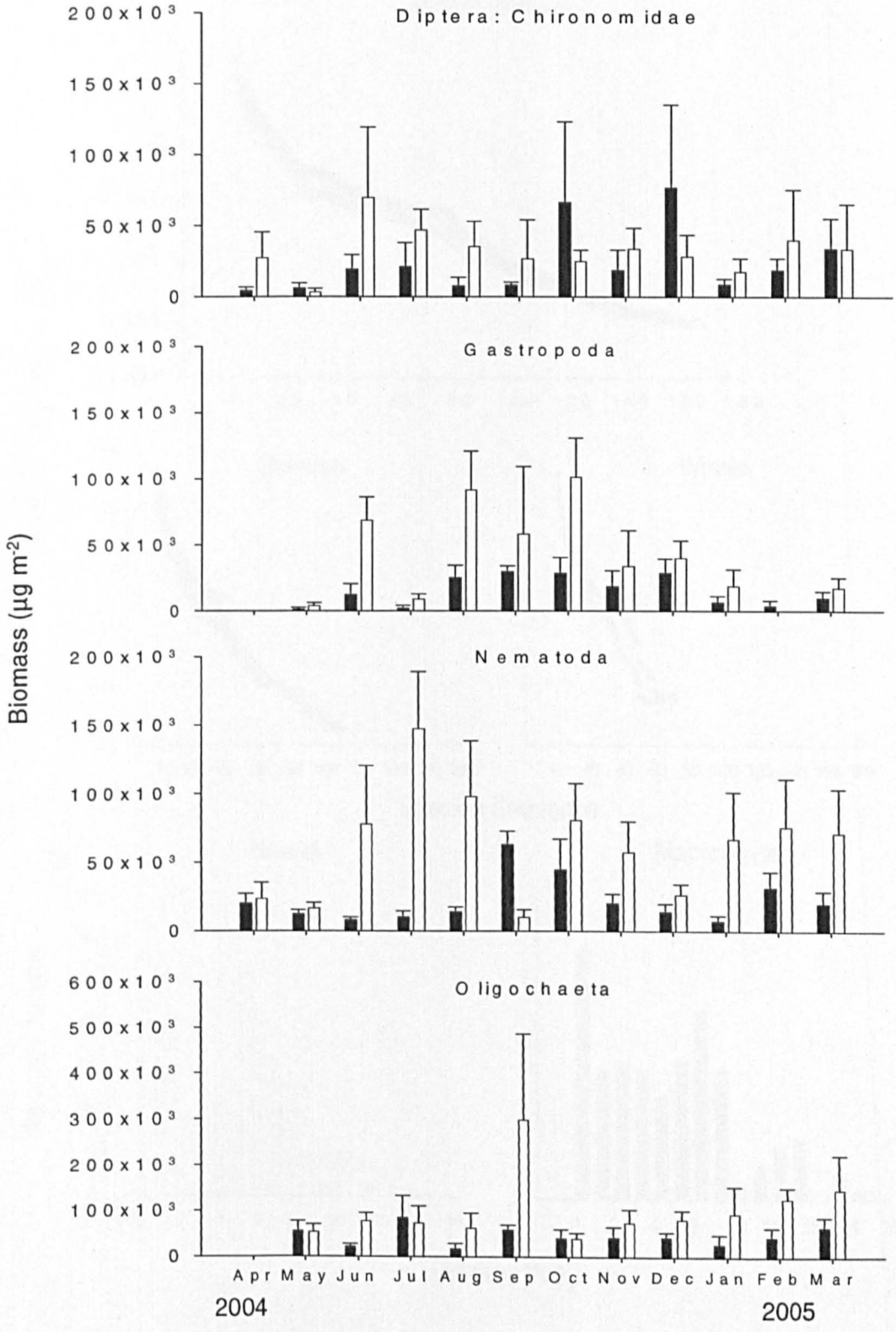

Figure 15. Monthly mean (±1 SE) biomass of the dominant meiofaunal groups; Diptera: Chironomidae, Gastropoda, Nematoda and Oligochaeta, within gravel beds (black bars) and macrophyte stands (white bars) (Note change of axis scale for Oligochaeta) of the River Lambourn between April 2004 and March 2005.

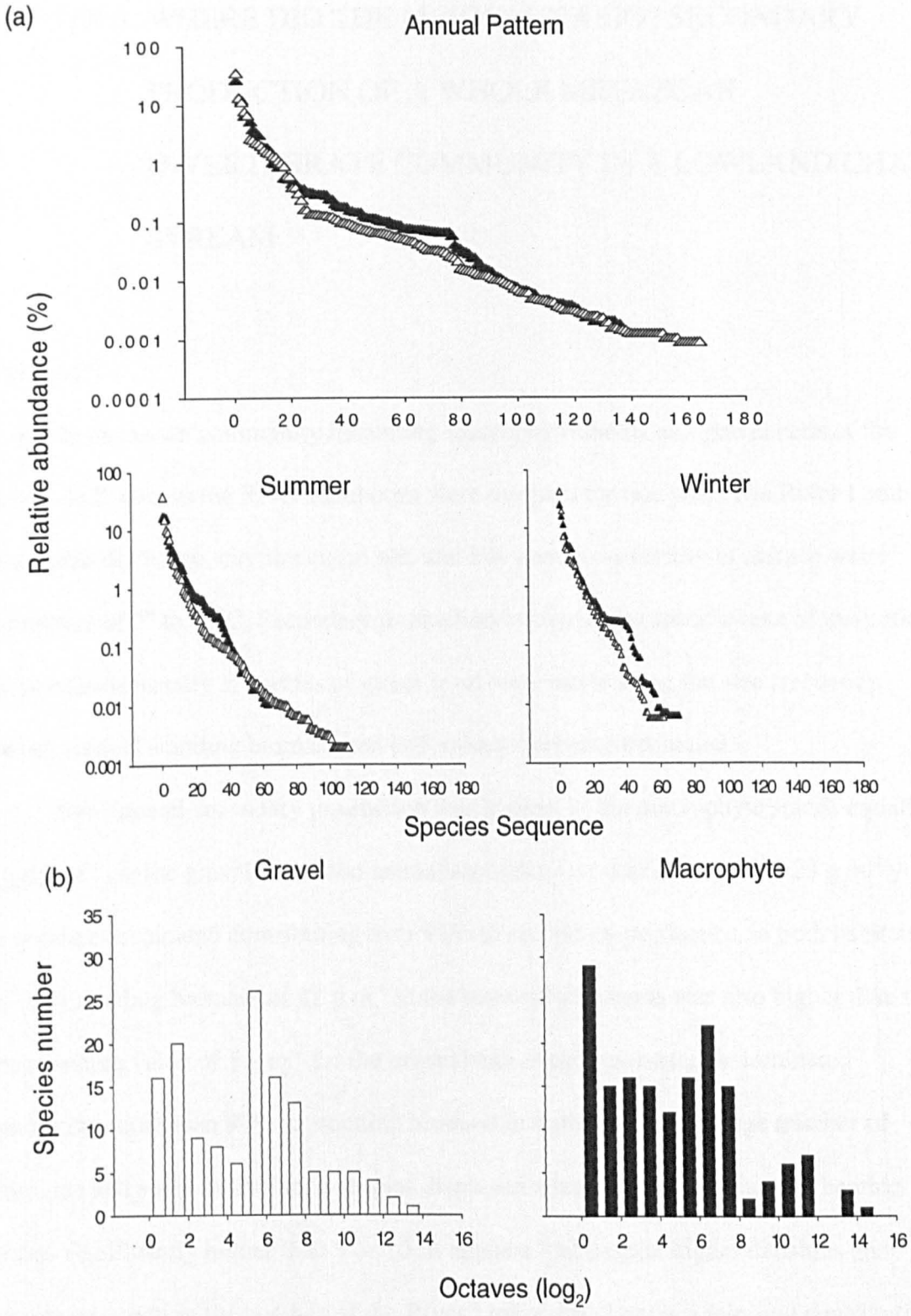

Figure 16. Species-abundance distributions of the invertebrate community in gravel beds (black triangles) and macrophyte stands (white triangles). (a) Annual, summer and winter percentage abundance distributions (spring and autumn not shown as they closely resembled summer and winter respectively). (b) Annual gravel and macrophyte log-normal distributions.

CHAPTER 3: WHERE DID THE MEIOFAUNA GO? SECONDARY PRODUCTION OF A WHOLE METAZOAN INVERTEBRATE COMMUNITY IN A LOWLAND CHALK STREAM

ABSTRACT

The whole metazoan community inhabiting macrophyte stands and gravel beds of the English chalk stream the River Lambourn were sampled for one year. The River Lambourn had a stable discharge, circumneutral pH, and low annual variability in surface water temperature of 7° to 15°C. Secondary production estimates for specific taxa of macrofauna and meiofauna usually at species or genus level were made using the size frequency method. Annual standing biomass and P/B values were also estimated.

Total annual secondary production was highest in the macrophyte stands equalling 65 g m^{-2} yr^{-1}, in the gravel beds total annual secondary production equalled 23 g m^{-2} yr^{-1}. Macrofauna dominated contributing over 91% to secondary production in both habitats. The total standing biomass of 12 g m^{-2} in the macrophyte stands was also higher than the corresponding value of 5 g m^{-2} for the gravel beds. Again macrofauna dominated contributing more than 97% to standing biomass in both habitats. A large number of meiofauna and some macrofauna species displayed annual P/B values in both benthic habitats significantly higher than 9 or 10. It appears that despite higher densities and turnover rates within the benthos of the River Lambourn, there is a minimal contribution of the meiofauna to total secondary production. The secondary production of this chalk stream is dominated by the macrofauna.

INTRODUCTION

Tansley (1935) formalised the concept of the "Ecosystem" which advocates studying biotic and physical components of an environment together rather than in isolation. Later, Lindeman (1942) synthesised the concept of an ecosystem with his own investigations of energy flow between trophic levels in lakes creating a conceptual framework for investigating the functioning of ecosystems. Energy flow can be measured in terms of production, within the heterotrophic consumers this is termed secondary production and can be defined as the total formation of biomass per unit time and area regardless of its fate (Benke, 1993). Production gives a comprehensive measure of "success" for a population or group as it encompasses many surrogate measures such as density, biomass, individual growth rate, reproduction, and survivorship (Benke, 1993). Therefore, estimates of secondary production allow us to assess the importance of different trophic or taxonomic groups to material and nutrient transfer within compartments of ecosystems, and to make comparisons across different systems.

The importance of the microfaunal community including bacteria and algae, in energy and material transfer within lotic systems is well recognised (Triska *et al.* 1989; Pusch *et al.* 1998). Furthermore the contribution to secondary production of macroinvertebrate taxa has also been documented through studies of individual species (Wotton, 1988; Alvarez and Pardo, 2005), trophic and taxonomic groups (Grzybkowska and Witczak, 1990; Pretty *et al.* 2005), and whole communities (Krueger and Waters, 1983; Benke *et al.* 1988). However, the importance of meiofauna (metazoans <0.5 mm) to total secondary production in lotic systems is still subject to debate.

Meiofauna are known to function as a link between trophic levels through feeding on basal resources and being prey to larger predators (Schmid and Schmid-Araya, 2002, Schmid-Araya *et al.* 2002a). However, due to their smaller size, on an individual basis

meiofauna should contribute much less to total biomass, and therefore may be expected to contribute less to total secondary production (Hakenkamp and Morin, 2000). Meiofauna, typically have faster generation times than macrofauna however, and occur at significantly higher benthic densities (Stead *et al.* 2003; Chapter 2); lotic studies have shown that meiofauna tend to be numerous reaching benthic densities of between 100,000 ind. m^{-2} (Stead *et al.* 2003), and 443,000 ind. m^{-2} (Bott and Borchardt, 1999). Moreover, estimates of total benthic biomass attributable to meiofauna range between 0.01% and 22% (Ramsay *et al.* 1997; Hakenkamp *et al.* 2002). Therefore, the potential significance of meiofauna to total stream secondary production is high.

Within lentic environments three separate studies found a high percentage contribution of meiofaunal size organisms to total metazoan production ranging from 33% to 60% (Holopainen and Paasivirta, 1977; Nalepa and Quigley, 1983; Strayer and Likens, 1986). In the few lotic studies reported so far, an even larger range has been found with meiofauna contributing between 0.07% and 52% of total metazoan production (Ramsay *et al.* 1997; Hakenkamp *et al.* 2002). In one of the most detailed studies of a whole metazoan community within a typically unproductive acid stream, Stead *et al.* (2005a) found that up to 51% of the total secondary production was due to meiofauna.

Hakenkamp and Morin (2000) postulated that higher contributions to total secondary production and biomass can be found from the meiofaunal size class in lotic environments where permanent as oppose to temporary taxa dominate. Temporary meiofauna taxa, especially insects, grow ten to one hundred times their initial juvenile size with most of their production occurring in the macrofaunal size class (Hakenkamp and Morin, 2000). Whereas permanent taxa complete their entire life cycle in meiofaunal size classes and consequently their production is never lost. Some evidence for the possible effect of meiofauna community taxonomic composition on biomass and production does

exist. Within Goose Creek where the meiofauna community is dominated by permanent taxa the total contribution to biomass of the size class is approximately 6% and production 50% (Poff *et al.* 1993). Whereas, in the Outaouais streams studied by Bourassa and Morin (1995) and Morin *et al.* (1995), the meiofauna community is dominated by insect taxa with the contribution of invertebrates less than 1mm to total invertebrate biomass equalling only about 1%, and production 3%.

In the Lone Oak stream, Stead *et al.* (2005a) reported a 51% contribution to total secondary production by the meiofauna community equalling 2.68 g m^{-2} yr^{-1} of the total annual secondary production of 5.22 g m^{-2} yr^{-1}. The contribution of permanent meiofauna taxa to total invertebrate production was only 15%, but significantly higher densities of meiofauna than macrofauna were found (Stead *et al.* 2003). Reiss (2006) revisited this acid stream and made a comparable estimate of 2.45 g m^{-2} yr^{-1} for meiofauna secondary production, which contrasted with a low estimate of ciliate production of 0.02 g m^{-2} yr^{-1} in the same stream. She also sampled a circumneutral, eutrophic stream and estimated secondary production of ciliates and meiofauna respectively of 4.45 and 21.17 g m^{-2} yr^{-1}. In a chalk stream for one taxon, *G. pulex*, with densities ranging between 800 and 10,000 ind. m^{-2} Welton (1979) estimated production of 12.8 g m^{-2} yr^{-1}, higher than the estimate for the entire metazoan community of the acid stream made by Stead *et al.* (2005a). Moreover, Baldock *et al.* (1983) estimated the production of ciliates for a chalk stream to be 1.83 g m^{-2} yr^{-1}.

Previously, a monthly survey of the whole metazoan community inhabiting macrophyte stands and gravel beds in the chalk stream, the River Lambourn, was carried out over one year (Chapter 2). A monthly mean macrofauna density range between 849 and 19,653 ind. m^{-2} similar to Welton (1979) for *G. pulex* was recorded. A similar pattern to Stead *et al.* (2003) was found for meiofauna with densities significantly higher than that of

macrofauna, ranging between 14,416 and 125,988 ind. m^{-2} (Chapter 2). In addition, densities of both macrofauna and meiofauna were significantly higher within macrophyte stands than the gravel beds (Chapter 2). Benke *et al.* (1984) and Benke and Parsons (1990) recognized the importance of habitat in influencing production values, whilst Smock *et al.* (1992) found differences in the macroinvertebrate production between debris dams and the hyporheic zone in two separate streams.

Because of the high reported densities and the habitat differences discussed in Chapter 2, the aim of this chapter was to estimate and evaluate the whole metazoan invertebrate secondary production for macrophyte stands and gravel beds within a chalk stream. The contributions to secondary production of the macrofauna, meiofauna, and specific taxonomic groups such as insects and non-insects are compared and assessed.

MATERIALS AND METHODS

Study area

The River Lambourn is a groundwater fed Cretaceous chalk stream which drains a highly permeable catchment dominated by agricultural land use within the Berkshire Downs of Southern England UK (51°25'29"N, 1°21'08"E). The Lambourn is hypernutrified, particularly with nitrate (Pretty *et al.* 2006), with a circumneutral pH ranging 7-8 (Chapter 2), and surface water temperature over the study duration between 7° and 15°C.

The study area was an 80 m reach of the north-channel at Bagnor, with a maximum recorded depth of 0.4 m, and a variable channel width between 3 and 6 m. The immediate riparian vegetation consisted of Salix *spp.* woodland on one side, and a wetland margin on the other. The stable discharge of the River Lambourn characteristic of chalk streams produced no well defined riffle-pool sequence on the streambed, but a gradual shift from areas of shallow fast flowing water dominated by coarser sediment (8 mm to 32 mm), to

areas with deeper and slower flowing water where 0.125 to 8mm sediment size were common (Pretty *et al.* 2006). Main streambed heterogeneity was caused by growth of discontinuous mixed stands of lotic macrophytes, mainly dominated by *Ranunculus spp.*, *Berula erecta* (Hudson) Coville, and *Callitriche spp.*

Sampling

Simultaneous quantitative benthic samples were taken monthly of meiofauna and macrofauna using a modified Hess sampler (surface area: 2.71 dm^2; mesh size 42 μm) from April 2004 through March 2005. Sampling was carried out as part of a wider study into surface-subsurface exchange in rivers (see Chapter 2; Pretty *et al.* 2006). Twelve modified Hess samples were taken each month except June 2004 where only seven samples were taken and July where eleven were taken due to logistical problems. Samples were taken at random, each from within a separate 2 m x 6 m grid of the streambed (see sampling design Chapter 2). Grids were spaced out evenly across the 80 m study reach and repeatedly sampled each month. Growth of lotic macrophytes was unpredictable over the spatial and temporal scale of the study so even sampling of the two habitats, gravel beds and macrophyte stands, was not possible. Therefore the presence or absence of lotic macrophytes was recorded monthly, samples pooled accordingly. Consequently 76 modified Hess samples were taken from gravel beds and 62 from macrophyte stands.

Hess samples were kept cool during transport to the lab where they were then separated into macrofauna fractions retained on a 500 μm sieve, and meiofauna fractions retained on a 42 μm sieve. Macrofaunal fractions were then preserved in ethanol for later counting and identification. All meiofaunal fractions were kept refrigerated and sorted live within one week of collection to ensure soft-bodied taxa were accounted for. After one

week mortality rates become too high in stored samples to represent densities of natural populations (Schmid-Araya, pers. comm.).

Individuals were measured to the nearest micrometer during enumeration and identification using either an Olympus BX50 (Olympus Optical, Tokyo, Japan) (1250x magnification) microscope, or a dissecting microscope (25-250x magnification), except Chironomidae and Oligochaeta which first had to be slide mounted in Euparal. Some highly abundant taxa (>30 individuals found in all samples from a substrate type in one month) were randomly subsampled and measured until a size frequency distribution with an acceptable level of sampling error set at 10% was achieved (Elliot, 1977). Measurements were converted to dry mass using published body length/ biovolume regressions and conversion factors (see Chapter 2 and Appendix 2). Further detailed description of the sampling design, sample processing and taxonomic designations can be found in Chapter 2.

Calculations of secondary production

Generation times are short and reproduction is continuous throughout the year for many meiofauna taxa including Nematoda (Traunspurger, 2002) and Microcrustacea (Galassi *et al.* 2002), both of which were common in the River Lambourn (see Chapter 2). Size frequency histograms for common macroinvertebrate taxa such as the chironomid genus, *Rheotanytarsus*, also revealed no discrete cohorts. The size frequency method of Hynes and Coleman (1968) which uses estimates of average cohorts was therefore deemed most appropriate to calculate production. In the method, life tables for specific taxa are constructed by creating 10 average cohorts (either body length or mass), determined by the size of the largest and smallest individual found during the sampling period. Then by calculating the changes in mean density of cohorts between different sampling dates combined with average cohort mass, a production can easily be derived by some

multiplication and addition (see Hynes and Coleman, 1968; Hamilton, 1969). To maintain consistency, the method was applied to all taxonomic groups regardless of whether discrete cohorts were identified. Within this study groups were divided into ten equal size classes based on body mass derived from regressions of body dimensions. All production estimates were made at the lowest practicable taxonomic level to reduce error associated with lumping species variable in maximum attainable body size and generation times (Hamilton, 1969; Benke 1979).

The size frequency method of Hynes and Coleman (1968) assumes an average cohort from all samples taken over a sampling period, in this case one year. However many taxa deviate from a 365 day generation time within the stream benthos. A correction factor is needed to account for parts of developmental growth of taxa which are not exclusively benthic dwellers, e.g. insect flight periods, and also taxa which develop either faster or slower than in the space of one year. This correction factor known as the Cohort Production Interval (CPI) was introduced by Benke (1979). CPIs were estimated using published life history data of minimum and maximum generation times for different taxonomic groups (see Appendix 4). Published life-history data which most closely matched the temperature range and taxonomic groups found within the River Lambourn were used. Three calculations of production were made, maximum, minimum and mean for the total metazoan community, meiofauna, macrofauna, various taxonomic groups and sub categories such as insects and non-insects.

RESULTS

Whole community comparisons

Total production within macrophyte stands for April 2004 to March 2005 ranged between 55.14 and 74.84 g dry weight m^{-2} yr^{-1} with a mean of 64.99 g dry weight m^{-2} yr^{-1} (Table 6).

Over the same time period within gravel beds total production ranged between 19.14 and 25.96 g dry weight m^{-2} yr^{-1} with a mean of 22.55 g dry weight m^{-2} yr^{-1}. Total standing biomass in the macrophyte stands of 11.87 g m^{-2} was also higher than the 5.13 g m^{-2} found in the gravel beds.

Estimates of production and standing biomass were much higher for macrofauna than meiofauna in both habitats, and higher for both size categories in macrophyte stands (Table 6). In macrophyte stands, macrofauna contributed 92.81% (60.32 g m^{-2} yr^{-1}) of the mean production and 97.5% of the standing biomass (11.58 g m^{-2}), whilst meiofauna contributed 7.19% (4.67 g m^{-2} yr^{-1}) and 2.5% (0.3 g m^{-2}) of the mean production and standing biomass respectively. In gravel beds, macrofauna contributed 91.62% (20.66 g m^{-2} yr^{-1}) to production and 97.27% to standing biomass (4.99 g m^{-2}), whilst meiofauna contributed 8.38% (1.89 g m^{-2} yr^{-1}) to production, and 2.73% (0.14 g m^{-2}) to standing biomass (Table 6).

Insects versus non-insects

The contribution of insect and non-insect groups to total metazoan production (Macrofauna + Meiofauna) and standing biomass in both habitats was fairly even. The largest difference was found in standing biomass of the gravel beds where the insect group contributed 57.9% and non-insect group 42.1% (Table 6). The contribution of insect and non-insect groups to production and standing biomass within the macrofauna strongly resembled the pattern of the whole metazoan community.

Within the meiofauna, non-insects contributed more to production and standing biomass than insect groups in both habitats. In the macrophyte stands, non-insects contributed 85.21% to production and 77.04% to standing biomass, whilst in the gravel beds they contributed 81.96% to production and 63.93% to standing biomass. However,

higher contributions of non-insects to meiofauna production and standing biomass did not translate into a higher contribution of permanent taxa. Temporary meiofauna taxa contributed noticeably more to production and standing biomass in both habitats, the greatest differences being found in gravel bed standing biomass were temporary taxa contributed 74.61% of the total.

Taxonomic group comparisons

Four taxa, Trichoptera, *G. pulex*, Gastropoda, and Simuliidae contributed 77.33% of the total production and 84.68% of the total standing biomass in macrophyte stands (Table 7). In the gravel beds *G. pulex*, Gastropoda, and Limoniidae contributed 78.75% of the total production and 90.40% of the total standing biomass (Table 7). Of the permanent meiofauna taxa, the nematodes made the highest contribution to total secondary production in both macrophyte stands and gravel beds (Table 7).

Examination of the production and standing biomass of taxonomic groups within the size fractions separately, revealed a very similar pattern for the macrofauna to that of the whole community with production and standing biomass concentrated in a few taxa, higher values occurring in the macrophyte stands (Table 8). In the meiofauna fraction, Oligochaeta contributed most to production in both habitats with 1.65 g m^{-2} yr^{-1} in the macrophyte stands and 0.61 g m^{-2} yr^{-1} in the gravel beds (Table 8). Oligochaeta were the only temporary taxa with higher production estimates for meiofauna (1.65 g m^{-2} yr^{-1}) than macrofauna (1.13 g m^{-2} yr^{-1}), however only in the macrophyte stands. Seven other groups contributed more than 0.1 g m^{-2} yr^{-1} to production in either habitat (Table 8). Four of these groups, the Nematoda, Harpacticoida, Acari and Microturbellaria belonged to the permanent meiofauna (Table 8).

P/B ratios

The lowest annual P/B ratios of 0.52 in the macrophyte stands and 0.35 in the gravel beds were both recorded for the group Astacidae. The highest annual P/B ratios were recorded for rotifer species, 208 for *Proales theodora* in the macrophyte stands (Appendix 5) and 347 for *Cephalodella gibba* in the gravel beds (Appendix 6). Within the family Chironomidae the most speciose group found within the River Lambourn, most species had annual P/B ratios less than 10. Of the five most dominant taxonomic groups in terms of production and biomass across the whole size range of the metazoan community (see Table 7), Limoniidae had the lowest annual mean P/B of 1.40 in the gravel beds. The highest annual mean P/B of any dominant taxa was 27.6 for Simuliidae also in the gravel beds. The annual mean P/B for the whole macrofauna community of 5.47 for the macrophyte stands was similar to the estimate of 4.39 for the gravel beds. Similarly the annual mean meiofauna community P/B ratios were higher, equalling 15.56 in the macrophyte stands and 13.5 in the gravel beds.

DISCUSSION

The higher estimates of secondary production and standing biomass in lotic macrophyte stands suggests the macrophytes are a more important benthic habitat than gravel beds for chalk stream invertebrates. Higher densities and P/B ratios were not sufficient to compensate for the much smaller body mass of meiofauna than macrofauna, resulting in a productivity dominance of larger taxa in this chalk stream. Permanent taxa did not dominate the meiofaunal size class and therefore taxonomic composition was not a satisfactory explanation for the low relative contribution of meiofauna to total secondary production. It would appear that meiofauna have a very limited role within the benthos of this aquatic system.

Differences between habitats and secondary production

Benke (1993) described streams with very high community productivity as usually organically enriched with invertebrate secondary production values in excess of 50 g m^{-2} yr^{-1}. Whilst Smock *et al.* (1992) have reported an invertebrate secondary productivity 5.5 times greater in organically enriched debris dam habitats when compared to sandy sediments in the same stream. Therefore, the macrophyte stand habitat within the River Lambourn with a secondary production of 64.99 g m^{-2} yr^{-1} should be considered highly productive most likely due to organic enrichment. Conversely, gravel beds with a lower secondary production of 22.55 g m^{-2} yr^{-1} should be considered a low productivity habitat with possibly limited availability of organic matter.

Lotic macrophytes are known to alter flow dynamics resulting in the increased deposition of sediment, including fine and coarse particulate organic matter (Hovarth,2004; Cotton *et al.* 2006), while positive relationships between organic matter and invertebrate densities of macrofauna and meiofauna have been previously established (Egglishaw, 1964; Silver *et al.* 2002). Organic matter provides a suitable substrate for colonisation, case-building, and also serves as food for many organisms (Wotton, 1994). However, within the River Lambourn only a weak non significant pattern of higher organic matter concentrations in macrophyte stands than gravel beds was found (Chapter 2). Despite no clear pattern of organic matter distribution, a higher density and biomass of invertebrates was found within the macrophyte stands and thus reflected upon production estimates.

Macrophyte stands may enhance the quality of the habitat for stream invertebrates in other ways, which could result in higher levels of secondary productivity. For example Fritz *et al.* (2003) have shown that macrophyte stands can increase substratum stability, reducing disturbance thereby allowing the establishment of larger populations of stream

invertebrates. Lotic macrophytes may also increase benthic habitat complexity and surface area through growth of stem and leaf architecture, potentially increasing habitable surface area for stream invertebrates and their food sources such as bacteria, fungi, and algae. Through increasing habitat complexity, macrophytes may also act as refugia from predation for invertebrates (Carpenter and Lodge, 1986; Harrison *et al.* 2005). Clearly productivity varies between habitats in the River Lambourn like in other streams and rivers (Benke *et al.* 1984; Smock *et al.* 1989).

Macrofauna production and other systems

Productivity values are also not uniform between separate streams and rivers (Benke, 1993). Chadwick and Huryn (2005) found no effect of increased nitrogen deposition on secondary production between two intermittent streams in adjacent catchments, whilst Cross *et al.* (2006) found that increased nutrient enrichment resulted in a 1.2 to 3.3 times higher secondary production in a headwater stream. Krueger and Waters (1983) demonstrated a positive association of macroinvertebrate secondary production with nitrate concentrations, alkalinity, and fish stocks, ranging from 8.125 to 33.1 g m^{-2} yr^{-1} dry mass across three different streams. Despite differences between streams, Mortensen and Simonsen (1983) estimated comparable macroinvertebrate secondary production of 31.68 g m^{-2} yr^{-1} in a spring-fed sandy stream which had vascular macrophytes intolerant of low pH, and also like Krueger and Waters (1983) a significant fish population.

The River Lambourn is a circumneutral chalk stream, hypernutrified from agricultural practices (Pretty *et al.* 2006), containing trout and grayling fisheries. Considering these environmental conditions, the secondary production values for the macroinvertebrates in the two habitats of 60.32 and 20.66 g m^{-2} yr^{-1} would appear to conform to published values. Moreover, the secondary production estimates of 14.12 and

4.65 g m^{-2} yr^{-1} within macrophyte stands and gravel beds respectively for *G. pulex* are similar to the only other secondary production estimates made for the same species in an English chalk stream Tadnoll Brook of 12.8 g m^{-2} yr^{-1} by Welton (1979).

Artefacts or real patterns?

In one of the few complete studies of secondary production incorporating meio- and macrofaunal size categories of invertebrates, Stead *et al.* (2005a) estimated a total mean meiofauna production of 2.68 g m^{-2} yr^{-1} and a standing biomass of 0.36 g m^{-2} for the oligotrophic acidic stream Lone Oak. Macrofauna production was low, equalling 4.46 g m^{-2} yr^{-1} with a standing biomass of 0.66 g m^{-2} yr^{-1}. Stead *et al.* (2005a) postulated two possible factors causing the low invertebrate secondary production in the Lone Oak: a) methodological assumptions when using the size-frequency method or b) the acidic character of the stream. Reiss (2006) revisited the Lone Oak and estimated secondary production of 2.45 g m^{-2} yr^{-1} for meiofauna using a combination of the interval biomass and increment summation methods; her estimate was very close to that of Stead *et al.* (2005a).

The Trichopteran *Agapetus spp.* was one of the few taxa for which discrete cohorts were identified in the River Lambourn. Comparison between the increment-summation and the size-frequency methods for estimating production of this group revealed a difference in production of less than 1 g m^{-2} yr^{-1} (S. Tod pers. obs). Whilst the estimates of macroinvertebrate production of 60.32 and 20.66 g m^{-2} yr^{-1} from macrophyte stands and gravel beds respectively were much higher than those of Stead *et al.* (2005a) but comparable with literature values, it seems likely that the production values obtained here and by Stead *et al.* (2005a) are not seriously confounded by methodological problems. The low macroinvertebrate production found by Stead *et al.* (2005a) is more likely due to the oligotrophic or acidic nature of the system which would conform to other published studies

into the effects of pH and nutrient status on production (Pretty *et al.* 2005; Gaedke and Kamjumke, 2006).

The relative contribution of meiofauna

In Mirror Lake, Strayer and Likens (1986) estimated the contribution of meiofauna to total zoobenthic production to be around 50%, whilst Holopainen and Paasivirta (1977) estimated 60% contribution in lake Pääjärvi. Similarly, Poff *et al.* (1993) estimated that meiofauna contributed 50% of the secondary production in a sandy stream, Goose Creek. While Stead *et al.* (2005a) reported a high percentage contribution of 51% for meiofauna to total secondary production in the Lone Oak. In contrast, Hakenkamp and Morin (2000) have asserted that meiofauna secondary production is generally less than 5% in lotic systems. Within the River Lambourn only between 7 and 9% of the total secondary production was contributed by meiofauna.

Hakenkamp and Morin (2000) postulated that the low relative contributions of meiofauna to total secondary production would most likely occur when the meiofauna community was dominated by temporary taxa. Within the River Lambourn the relative contribution of meiofauna to total secondary production was low and the contribution of permanent meiofauna taxa to total meiofauna secondary production was only around 38% to 41%. Furthermore, the relative contribution of insect taxa to secondary production within the meiofauna size class across the two habitats was only approximately 14% to 18%, whereas in the macrofauna size class it significantly increased to around 46% to 52%. The findings are consistent with Hakenkamp and Morin (2000) in their assertion that meiofauna are more important to overall secondary production when the community is dominated by permanent taxa. It would seem insect taxa only contribute significantly to production in larger size classes.

In contrast, Stead *et al.* (2005a) found no evidence linking the high contribution of meiofauna to total stream invertebrate secondary production in the Lone Oak to the dominance of permanent taxa. They found the highest contribution to meiofauna secondary production of around 57% for oligochaetes, this pattern of oligochaete dominance was later confirmed by Reiss (2006). Stream studies by Bourassa (1993) on log median particle diameter and Nadon (1993) on periphyton biomass have shown an effect on the relative contribution of meiofauna to total secondary production which could explain the varying patterns of meiofauna contribution to total secondary production in different streams.

However, Poff *et al.* (1993) concluded that the lack of a riffle-pool sequence for macroinvertebrates, and the dominance of sandy substrata may have favoured meiofaunal size invertebrates resulting in the unusual contribution in Goose Creek. The data presented here indicated no methodological problems in the study of Stead *et al.* (2005a). However, similarly to Poff *et al.* (1993), an exclusion of macrofauna did occur probably due most likely to the prevailing environmental conditions of oligotrophy and low pH in the Lone Oak. It is probable the lack of macrofauna caused an unusually high relative contribution of meiofauna to secondary production in the Lone Oak. Consequently, the assertion of Stead *et al.* (2005a) that excluding meiofauna from production studies could severely underestimate total benthic secondary production by up to 50% may only be true for acidic streams or possibly ones where the macrofauna production is low.

Meiofauna production in relation to other systems

Meiofauna secondary production in macrophyte stands of the River Lambourn was only 1.75 times greater than in the Lone Oak, whilst meiofaunal production in the gravel beds was 1.29 times lower than in the Lone Oak. These estimates are consistent with the comparable peaks in the monthly mean benthic densities of meiofauna, of 120,000 ind. m^{-2}

(Chapter 2) from the River Lambourn, and 100,000 ind. m^{-2} reported by Stead *et al.* (2003) for the Lone Oak. It seems intriguing that the meiofauna secondary production remains fairly constant between the oligotrophic acidic Lone Oak and eutrophic circumneutral River Lambourn.

Moreover, Reiss (2006) estimated meiofauna secondary production from a nutrient rich circumneutral stream, The Pant, in southern England, where total meiofaunal secondary production was approximately 21 g m^{-2} yr^{-1}, which is significantly higher than any of the estimates in the eutrophic River Lambourn. However surface water nitrate concentrations in the Pant were approximately 4 times higher than the 400-500 μM reported by Pretty *et al.* (2006) for the River Lambourn. Moreover, the River Lambourn estimate of macrophyte stand meiofauna secondary production was 4.5 times lower than that of the Pant.

Gaedke and Kamjunke (2006) reported significantly higher biomass and production of zooplankton, mainly due to rotifers and small crustaceans, in eutrophic rather than oligotrophic lakes. Whilst Mirror Lake, where Strayer and Likens (1986) estimated a 50% contribution of meiofauna to total secondary production was highly eutrophic. In marine seagrass beds, Danovaro *et al.* (2002) estimated total meiofauna secondary production values of between 18.75 and 33 g m^{-2} yr^{-1} values significantly higher than any estimate for a stream or river so far. These estimates of benthic densities, biomass and secondary production suggest that production values for meiofauna far in excess of this study and possibly that of Reiss (2006) could yet be found. It is clear that more comparative estimates of production are needed in order to establish what really limits the secondary production of meiofauna in different systems and what environmental conditions are optimal for them.

P/B ratios and production

Metabolic theory predicts that larger species in terms of body mass are expected to have slower development, generation times and metabolism, resulting in lower production/biomass ratios (Brown and Gillooly, 2003). Consequently macrofauna should have lower P/B ratios than meiofauna. However, McIntyre (1964) made a very low estimate for the annual P/B of temperate marine meiofauna of around 10; later Gerlach (1971) made an estimate for marine nematodes of 9. Whilst Waters (1977) reviewing P/B data in the literature for freshwater fauna including macrofaunal and meiofaunal invertebrates concluded that values greater than 10 are rare.

Similarly to Stead *et al.* (2005a) higher P/B ratios for meiofauna than the macrofauna consistent with the expectations of metabolic theory were found. Stead *et al.* (2005a) and Reiss (2006) both frequently found meiofauna with P/B values significantly higher than 9 to 10. Within the River Lambourn a diverse array of species from turbellarians, to rotifers and insects had P/B values greater than 9 to 10. In a study of 207 marine benthic macroinvertebrate taxa encompassing a global distribution, Cusson and Bourget (2005) found a P/B range of between 0.0035 and 36.7. Huryn and Wallace (2000) have reported a range of P/B values for stream insects between 1 and 117, whilst Benke (1998) has found some of the highest P/B values for chironomids ranging from 158 to 258. Clearly P/B ratios higher than 9 to 10 are not rare as previously thought.

Conclusions

In conclusion the findings suggest despite occurring at higher densities, with higher metabolic rates, faster generation times and higher P/B ratios, body size probably constrains the contribution to secondary production of the meiofauna in the River Lambourn. Within chalk streams, meiofauna contributions to benthic secondary production may well only

exceed those of macrofauna under exceptional conditions where macrofauna are excluded or restricted. The assertion of Hakenkamp and Morin (2000) that meiofauna are generally of limited importance to the benthic secondary production of lotic environments may appear to be true. However, caution must be applied in interpreting these findings as the potential significance of meiofauna to total lotic system secondary production may well be underestimated by studies which focus solely on the streambed surface. Meiofauna can vastly outnumber macrofauna in hyporheic sediments adjacent to stream channels (Schmid-Araya, 1997; Stead *et al.* 2004) which could significantly increase their potential significance to total stream invertebrate secondary production possibly beyond that of macrofauna.

Table 6. Production and standing biomass (dry weight) estimates for the metazoan community from macrophyte stands and gravel beds, of the river Lambourn between April 2004 and March 2005. Groups for comparisons are; permanent and temporary meiofauna; total meiofauna and macrofauna insects and non-insects, total insects and non-insects; and total meiofauna and macrofauna. For each habitat mean, minimum and maximum production and total standing biomass for each group are shown, along with percentage of total production and standing biomass.

	Macrophyte						Gravel					
	Production (g m^{-2} yr^{-1})				Standing biomass		Production (g m^{-2} yr^{-1})				Standing biomass	
Metazoan Community	Mean	(%)	Min	Max	(g m^{-2})	(%)	Mean	(%)	Min	Max	(g m^{-2})	(%)
Meiofauna (passing through a 500 µm sieve)												
Insect	0.69	14.79	0.47	0.91	0.07	22.96	0.34	18.04	0.24	0.44	0.05	36.07
Non-insect	3.98	85.21	2.75	5.21	0.23	77.04	1.55	81.96	1.05	2.04	0.09	63.93
Permanent	1.81	38.75	0.71	2.91	0.09	28.80	0.76	40.25	0.31	1.21	0.04	25.39
Temporary	2.86	61.25	2.51	3.21	0.21	71.20	1.13	59.75	0.98	1.28	0.10	74.61
Total	4.67	7.19	3.22	6.12	0.30	2.50	1.89	8.38	1.29	2.49	0.14	2.73
Macrofauna (retained on a 500 µm sieve)												
Insect	31.17	51.68	26.66	35.68	5.70	49.21	9.61	46.53	8.41	10.81	2.92	58.51
Non-insect	29.15	48.32	25.26	33.03	5.88	50.79	11.05	53.47	9.44	12.66	2.07	41.49
Total	60.32	92.81	51.92	68.71	11.58	97.50	20.66	91.62	17.85	23.47	4.99	97.27
Macrofauna + Meiofauna												
Insect	31.86	49.03	27.13	36.60	5.76	48.55	9.95	44.14	8.65	11.26	2.97	57.90
Non-insect	33.13	50.97	28.01	38.24	6.11	51.45	12.60	55.86	10.49	14.71	2.16	42.10
Total	64.99		55.14	74.84	11.87		22.55		19.14	25.96	5.13	

Table 7. Annual production and standing biomass estimates for the whole metazoan community (meiofauna plus macrofauna) from each habitat. Taxa have been ordered highest mean production first within the most productive habitat type. Values for mean, minimum, and maximum production, standing biomass, and percentage of total production and biomass are shown.

	Macrophyte						Gravel					
	Production ($g\ m^{-2}\ yr^{-1}$)				Standing biomass		Production ($g\ m^{-2}\ yr^{-1}$)				Standing biomass	
	Mean	(%)	Min	Max	($g\ m^{-2}$)	(%)	Mean	(%)	Min	Max	($g\ m^{-2}$)	(%)
Trichoptera	15.42	23.73	15.28	15.56	3.97	33.40	3.04	13.49	2.91	3.18	0.47	9.21
Gammarus pulex	14.12	21.73	13.83	14.42	4.12	34.74	4.65	20.61	4.55	4.75	1.26	24.53
Gastropoda	13.44	20.68	9.75	17.13	1.44	12.09	5.65	25.06	4.10	7.20	0.59	11.51
Simuliidae	7.27	11.19	3.35	11.19	0.53	4.45	1.38	6.12	0.64	2.12	0.05	0.91
Limoniidae	5.49	8.45	5.49	5.49	0.89	7.54	3.11	13.78	3.11	3.11	2.21	43.04
Oligochaeta	2.78	4.28	2.78	2.78	0.24	2.01	1.44	6.39	1.44	1.44	0.13	2.59
Ephemeroptera	2.30	3.53	1.90	2.69	0.20	1.65	1.03	4.56	0.74	1.31	0.07	1.31
Nematoda	1.40	2.16	0.56	2.25	0.06	0.52	0.45	1.99	0.18	0.72	0.02	0.42
Chironomidae	0.98	1.50	0.69	1.26	0.10	0.84	0.36	1.60	0.25	0.48	0.05	0.93
Cladocera	0.66	1.02	0.66	0.66	0.01	0.10	0.005	0.02	0.00	0.00	0.00	0.003
Elmidae	0.31	0.48	0.31	0.31	0.06	0.48	0.08	0.35	0.08	0.08	0.02	0.30
Hirudinea	0.22	0.33	0.20	0.24	0.06	0.49	0.04	0.18	0.04	0.04	0.02	0.29
Harpacticoida	0.19	0.30	0.11	0.27	0.02	0.13	0.14	0.64	0.09	0.20	0.01	0.21
Acari	0.17	0.26	0.02	0.32	0.01	0.06	0.03	0.13	0.00	0.06	0.00	0.01
Astacidae	0.09	0.14	0.08	0.10	0.15	1.30	0.05	0.22	0.05	0.05	0.13	2.48
Ceratopogonidae	0.09	0.13	0.09	0.09	0.02	0.18	0.12	0.54	0.10	0.15	0.02	0.30
Microturbellaria	0.03	0.04	0.006	0.045	0.001	0.004	0.12	0.54	0.031	0.215	0.002	0.05
Rotifera	0.007	0.01	0.0061	0.0086	0.0001	0.001	0.01	0.05	0.0098	0.0139	0.0001	0.002
Cyclopoida	0.007	0.01	0.0045	0.0096	0.0004	0.003	0.001	0.01	0.0009	0.0020	0.0001	0.002
Plecoptera	0.006	0.01	0.005	0.008	0.001	0.01	0.83	3.70	0.835	0.835	0.097	1.90
Tardigrada	0.0005	0.001	0.0001	0.0009	0.0001	0.0005	0.0005	0.002	0.0001	0.0008	0.0000	0.0004
Ostracoda	0.0005	0.001	0.00034	0.00057	0.00004	0.0003	0.002	0.01	0.00123	0.00205	0.00005	0.001
Gastrotricha	0.00	0.00	0.00	0.00	0.00	0.00	0.00005	0.0002	0.00	0.00	0.00	0.00002
Total	64.99		55.14	74.84	11.87		22.55		19.14	25.96	5.13	

Table 8. Production and standing biomass estimates for taxa within the two size fractions from each habitat. Taxa have been ordered according to highest mean production first in macrophyte stands. Mean production and standing biomass estimates are given.

	Macrophyte		Gravel	
	Mean production ($g\ m^{-2}\ yr^{-1}$)	Standing biomass ($g\ m^{-2}$)	Mean production ($g\ m^{-2}\ yr^{-1}$)	Standing biomass ($g\ m^{-2}$)
Macrofauna (retained on a 500 µm sieve)				
Trichoptera	15.42	3.97	3.04	0.47
Gammarus pulex	14.08	4.11	4.63	1.25
Gastropoda	12.98	1.40	5.49	0.58
Simuliidae	7.07	0.51	1.35	0.04
Limoniidae	5.49	0.89	3.11	2.21
Ephemeroptera	2.28	0.19	1.01	0.06
Oligochaeta	1.13	0.14	0.83	0.10
Cladocera	0.65	0.01	0.00	0.00
Chironomidae	0.57	0.07	0.10	0.01
Elmis sp.	0.31	0.06	0.08	0.02
Hirudinea	0.22	0.06	0.04	0.02
Astacidae	0.09	0.15	0.05	0.13
Ceratopogonidae	0.02	0.01	0.09	0.01
Plecoptera	0.01	0.001	0.83	0.10
Total	60.32	11.58	20.66	4.99
Meiofauna (passing through a 500 µm sieve)				
Oligochaeta	1.65	0.09	0.61	0.04
Nematoda	1.40	0.06	0.45	0.02
Gastropoda	0.46	0.04	0.16	0.01
Chironomidae	0.41	0.03	0.26	0.04
Simuliidae	0.20	0.02	0.03	0.002
Harpacticoida	0.19	0.02	0.14	0.01
Acari	0.17	0.01	0.03	0.0007
Ceratopogonidae	0.07	0.01	0.03	0.01
Gammarus pulex	0.05	0.01	0.02	0.01
Microturbellaria	0.03	0.001	0.12	0.002
Cladocera	0.02	0.002	0.005	0.0001
Ephemeroptera	0.02	0.002	0.02	0.003
Rotifera	0.01	0.0001	0.01	0.0001
Cyclopoida	0.01	0.0004	0.001	0.0001
Trichoptera	0.003	0.001	0.002	0.001
Tardigrada	0.0005	0.0001	0.0005	0.00002
Ostracoda	0.0005	0.00004	0.002	0.00005
Plecoptera	0.00	0.00	0.0004	0.0001
Gastrotricha	0.00	0.00	0.00005	0.000001
Total	4.67	0.30	1.89	0.14

CHAPTER 4: A HIGHLY RESOLVED CHALK STREAM BENTHIC FOOD WEB: STABLE ISOTOPE ANALYSIS REVEALS THE FUNCTIONAL IMPORTANCE OF MEIOFAUNA

ABSTRACT

Dual, gut content and stable isotope analysis were used to investigate seasonal food webs for the invertebrate community of the River Lambourn, a chalk stream in southern England. A high level of taxonomic resolution was used in gut content food webs with difficult meiofaunal groups and basal diatom species resolved to genus and/or species. A modified stable isotope technique with a reduced column was used to obtain stable isotopic signatures of lotic meiofauna for the first time.

Gut content analysis indicated that the stream community was dependent on both autochthonous and allochthonous carbon sources. Distinct seasonal variation between spring/summer and autumn/winter food webs was found. Web size ranged from 77 to 133 and number of links from 266 to 817, from winter to summer respectively. There was a negligible amount of trophic overlap in the webs and directed connectance remained low and constant ranging between 0.042 and 0.046. Intermediate species dominated with proportional contributions to web size ranging between 0.481 and 0.556. High proportions of basal species were also found ranging between 0.354 and 0.454, with the intermediate-basal proportion of total links of between 0.794 and 0.915 dominating.

The stable isotope analysis strongly reflected the gut content data with significant contributions of both autochthonous and allochthonous food sources to the diet of meiofaunal taxa being indicated. Moreover, seasonal variation in isotopic signatures for

some taxa was found. Isotope data indicated a low number of trophic levels in the food web and an indistinct diet for the meiofauna community from that of the macrofauna.

Generalist feeding of both macroinvertebrates and meiofauna with similar trophic positions suggest that meiofauna and macrofauna can be lumped together when investigating the functional role of invertebrates in streams and rivers. For the River Lambourn combined analysis of both meio- and macroinvertebrates demonstrated a high degree of plasticity in feeding. Species fed upon food items well outside the constraints of their expected diet spectrum based on membership of traditional functional feeding categories. The data for the River Lambourn fit most closely to the original River Productivity Model of Thorp and Delong (1994). Crucially the findings indicate accurate determination of autotrophic-heterotrophic balances in streams and rivers need to incorporate some measure of meiofauna functional roles.

INTRODUCTION

In depicting "entangled banks" Darwin (1859) was the first to formally recognise and discuss the significance of the high levels of complexity attained by natural communities. To manage these levels of complexity when investigating energy flow, stability, and other general properties of communities, ecologists have used the food web approach and reduce complexity through investigating subsets of webs (Dawah, 1995; Jepsen and Winemiller, 2002) or lumping species together (Briand, 1983; Martinez *et al.* 1999). Cummins (1974) combined both approaches to produce a simplified diagram representing a headwater stream community where invertebrates were classified into the functional feeding groups: predators; shredders, which feed on coarse particulate organic matter (CPOM); collectors, which feed on fine particulate organic matter (FPOM); and scrapers, which feed on algae and other microproducers.

However, communities are not isolated, transfers of nutrients, detritus and organisms occur (Polis *et al.* 1997) and some empirical evidence exists for this transfer (Polis and Hurd 1996, Ben-David *et al.* 1997). By incorporating functional feeding groups into their River Continuum Concept (RCC) Vannote *et al.* (1980) recognised this. They attempted a holistic view of lotic ecosystem energy flow predicting a continuum through heterotrophy to autotrophy and back to heterotrophy from small headwater streams to large rivers. Changes in functional feeding groups should reflect the continuum where headwater streams (order 1-3) maybe dominated by shredders and collectors feeding on CPOM and FPOM, respectively. Medium sized streams (order 4-6) are predicted to consist mainly of collectors feeding on FPOM and grazers and scrapers feeding on autochthonous sources, with large rivers (>7 order) dominated by collectors feeding on FPOM derived from upstream (Vannote *et al.* 1980).

Refinements to the RCC have led to the Serial Discontinuity Concept of Ward and Stanford (1983) which incorporates the effects of large dams and reservoirs, and the Flood Pulse Concept of Junk *et al.* (1989) which proposes a significant role of floodplain detritus in higher order rivers. None of the former concepts, including the RCC, incorporated local autotrophic production as an important food source. In response to this Thorp and Delong (1994) proposed the Riverine Productivity Model (RPM) where large rivers possess a significant autotrophic component.

Applying models such as the RCC or RPM to streams and rivers can be problematic though as it is often difficult to accurately distinguish functional feeding groups (Zah *et al.* 2001). Long before functional feeding groups or guilds were formalised by Cummins (1974) and others, plasticity of feeding had been documented (Slack, 1936; Jones, 1950). Cummins (1974) described the consumption of algae and detritus by predators and animal prey by other functional feeding groups as fortuitous. Lancaster *et al.* (2005) suggested that the poor understanding of feeding and nutrition in freshwater invertebrates may be due to many researchers overlooking or ignoring unusual gut contents. Many gut content analyses since the conceptualisation of functional feeding guilds have documented ubiquitous plasticity of feeding in freshwater macroinvertebrates (Feminella and Stewart, 1986; Malmqvist *et al.* 1991; Helms and Creed, 2005).

Stable Isotope Analysis (SIA) is potentially a more powerful technique for determining feeding links as it measures animal tissue and relates it to food resources. Consequently, not only is the ambiguity of food resources which are ingested but not assimilated removed, but unlike gut content analysis an indication of the average feeding behaviour of an organism per unit time of tissue turnover is estimated (Gearing, 1991). Furthermore, because consumers become enriched in $\delta^{15}N$ by 3 to 4‰ and $\delta^{13}C$ by only 0 to 1‰ relative to their food sources, nitrogen and carbon stable isotope ratios are suitable

for accurate determination of the trophic position and food sources of consumers respectively (Post, 2002). In conjunction with examination of gut contents, SIA provides a powerful tool to determine the feeding and trophic position of organisms (Peterson and Fry, 1987).

Combined gut content and SIA has been used successfully to study freshwater invertebrates in many lentic (Gu *et al.* 1994; Hecky and Hesslein, 1995; Jones and Waldron, 2003) and lotic systems (McArthur and Moorhead, 1996; Huryn *et al.* 2001; Jardine *et al.* 2005), and to demonstrate high plasticity of feeding for some stream invertebrate communities (Zah *et al.* 2001; Lancaster *et al.* 2005). With regard to riverine theories, concepts and models, SIA has been used to demonstrate the overriding importance of both autotrophic and heterotrophic production in different systems (McCutchan and Lewis, 2002, Thorp and Delong, 2006). Finlay (2001) compiled data from 70 sites and 26 published studies on SIA and found that a transition from a reliance on terrestrial detritus to algae occurred for consumers in watersheds $\geq$10 km^2. This suggests production of higher trophic levels is decoupled from the detrital food web in larger streams and rivers.

A significant number of combined gut content and stable isotope analyses conducted into the food webs of large rivers around the globe reviewed by Thorp and Delong (2002) have also favoured autotrophic production. Consequently, Thorp and Delong (2002) revised the RPM downplaying the significance of heterotrophic carbon sources. The redefined RPM contains two significant energy pathways through the food web of 4th order rivers or greater: the algal-grazer pathway, and the decomposer pathway which includes the microbial loop. Within the microbial loop of the RPM an unclear role for rotifers is mentioned, however to date the functional role of the meiofauna (metazoans <0.5mm) has been largely ignored. This probably reflects the slow development of

freshwater meiofauna research, a lack of understanding about their trophic position in webs, and their functional role (Hakenkamp and Morin, 2000; Schmid-Araya and Schmid, 2000).

In the concept of functional feeding groups, Cummins (1974) defined microfauna as including, diatoms, algae, and meiofauna which formed part of the FPOM consumed by larger invertebrates. Cummins (1974) dismissed the importance of most microconsumers other than bacteria, fungi, protozoans and diatoms due to their apparent low biomass. However, various studies have demonstrated a high contribution of meiofauna to total metazoan density, biomass and production in some lotic systems (Hakenkamp *et al.* 2002; Stead *et al.* 2003; Stead *et al.* 2005a; Chapter 2). Moreover, higher tissue turnover and metabolic rates for meiofauna than macrofauna have been demonstrated indicating their smaller size may not negate some significant contribution to functioning of lotic systems (Benke, 1993; Reiss, 2006; Chapter 3).

Meyer (1994) expanded upon the food web of Cummins (1974) defining the position and trophic transfers involved in the microbial loop of headwater streams. This new food web was parsimonious with the RCC in deriving its main energy input from allochthonous material (Fig. 17). Within this general web, the meiofauna consume bacteria, CPOM, fungi, algae, flagellates and ciliates, but mainly detritus, and are then consumed along with FPOM by the macroinvertebrates.

However, a number of authors have reported variable diets for lotic meiofauna, individuals grazing solely on bacteria, detritus, diatoms, or mixtures of food items (Perlmutter and Meyer, 1991; Meyer, 1994; Borchardt and Bott, 1995; Bott and Borchardt, 1999). Moreover work by Schmid-Araya *et al.* (2002a) found that resolving for the meiofauna in the food web of an acid stream significantly changed general web properties and indicated a significant predatory or omnivorous aspect to their feeding which is supported by an ever growing body of research (see review by Schmid-Araya and Schmid,

2000). The simplistic headwater stream food web of Meyer (1994) may not apply to larger streams and rivers where a greater variety of resources are available.

SIA investigations of meiofauna are rare and have mainly been conducted in marine and brackish systems (Couch, 1989; Middleburg *et al.* 2000; Romanuk *et al.* 2006). Only one tracer experiment utilising SIA in a lotic system has occurred (Hall and Meyer, 1998). This paucity of research is probably due to difficulties in collecting sufficient numbers of individuals for analysis free of contaminants such as organic matter lodged in body hairs (Riera *et al.* 1996). Within the few studies conducted, some notable successes have been made including: a) confirmation that intertidal nematodes feed on microphytobenthos (Riera *et al.* 1996); b) seasonal and between species variability in isotopic signatures related to food resources (Carman and Fry, 2002); c) increased stability of meiofauna populations with more generalist feeding (Romanuk *et al.* 2006); and d) estimates with isotopic tracers that stream harpacticoids derive over 50% of their carbon from bacteria (Hall and Meyer, 1998).

In this chapter, a unique dual gut content and stable isotope analysis of meiofauna from a lowland chalk stream is presented. Taxonomically challenging groups such as diatoms and meiofauna are resolved to genus and species wherever possible providing one of the most complete descriptions of a stream invertebrate food web to date. Because food webs with this level of resolution are rare, general properties of the food webs are presented and discussed, as well as an exploration of the effects of different levels of taxonomic resolution. SIA and gut content data are compared and discussed. Finally a new simplified food web adapted from Meyer (1994) is described to represent the invertebrate community found in the chalk stream system studied.

MATERIALS AND METHODS

Study Site

The River Lambourn is a lowland Cretaceous chalk stream that drains a rural catchment (234 km^2) of southern England dominated by agricultural practices. The stream is hypernutrified (Pretty *et al.* 2006) with a circumneutral pH 7-8 (Chapter 2). Most rainfall in the catchment is absorbed into the chalk aquifer reaching the main channel as upwelling groundwater. Hence the river has a stable discharge and no well-defined riffle-pool sequence. There is one surface tributary in the catchment, the Winterbourne Stream, which confluences with the north channel of the River Lambourn 10 m upstream from the study site at Bagnor ($51^0$25'29"N, $1^0$21'08"E).

The study site was an 80 m reach with a channel width varying between 3 and 6 m and a maximum depth of 0.4 m. Mean surface water temperature at the study site ranged between 8.4 and 15.4^{0}C, and conductivity was stable around 470 to 540 µS cm^{-1}. Main riparian vegetation adjacent to the left side of the study site consisted of a wetland, and to the right side a *Salix* spp. dominated woodland. Most bed heterogeneity is caused by mixed stands of instream macrophytes, mainly *Ranunculus spp.* and *Berula erecta* (Hudson) Coville.

Sampling

Quantitative sampling of the streambed was carried out with a modified Hess sampler (surface area: 2.71 dm^2; mesh size 42 µm) between April 2004 and March 2005, as part of a wider study into the nutrient dynamics of streams and rivers (see Chapter 2; Pretty *et al.* 2006). Twelve samples were taken at random each month, from within twelve separate 2 m x 6 m grids of the streambed spaced evenly across the field site. Due to logistical problems during the year 2004 only seven samples were taken in June, and eleven in July. Over the

temporal and spatial scale of the study growth of lotic macrophytes was unpredictable. It was therefore impossible to ensure availability of habitat for even sampling of gravel beds and macrophyte stands throughout the study duration. Consequently, the presence or absence of lotic macrophytes in samples was recorded and they were then separated accordingly, resulting in a total of 76 gravel bed samples and 62 macrophyte stand samples.

Samples were kept cool during transport to the lab where they were sieved into size fractions of meiofauna (>42 μm-<500 μm) and macrofauna (>500 μm). The macrofauna fraction was immediately preserved in ethanol for later sorting and counting. Meiofauna fractions were kept refrigerated, counted and sorted live within one week of collection as after seven days mortality rates in stored samples exceed acceptable levels to represent natural densities of field populations (Schmid-Araya, pers. comm.).

As macrophyte stands supported a significantly higher density, biomass, and species richness of invertebrates than gravel beds (see Chapter 2), it was decided to only use invertebrate samples from macrophyte stands to construct benthic food webs. Monthly macrophyte stand samples were split into four seasons: spring (Mar-May), summer (Jun-Aug), autumn (Sep-Nov), and winter (Dec-Feb), resulting in a minimum of 14 and maximum of 19 replicates. This procedure allowed for an increase in resolution of diet spectra for uncommon and rarer taxa.

Gut content analysis

After enumeration all invertebrates were identified to the lowest practicable taxonomic level, usually species. For Chironomidae, Oligochaeta, and Copepoda this was done after slide mounting with Euparal. Feeding interactions were identified by gut content analyses of all invertebrate specimens found for rare and uncommon taxa. Macroinvertebrate taxa such as Ephemeroptera, Simuliidae, and late instar chironomids were decapitated,

dissected, and their gut contents fixed with Euparal or glycerol on microscope slides, smaller meiofaunal taxa were mounted whole. Slides were then examined under a binocular microscope at 1000x magnification with oil immersion to identify prey remains following Schmid and Schmid-Araya (1997). Whole mount reference slides, data on known species for the site (see Chapter 2), and taxonomic keys were used to identify gut contents. Diatom species were resolved from the diet content of invertebrate taxa spread out on the whole mount reference slides. Identification was only carried out on fully intact diatom specimens that showed clear diagnostic characteristics at 100x and 200x magnification from thinly spread sections of diet content on whole mount reference slides. The total number of individual invertebrates used for gut examination for each season equalled 356 in spring, 562 in summer, 284 in autumn, and 182 in winter.

Web properties and functional feeding groups

Four seasonal food web matrices and a summary web were constructed. In order to investigate the effect of taxonomic resolution on food webs two further matrices of the summer web were constructed, one with diatoms poorly resolved hereafter referred to as the *Basal web*, and another with intermediate species unresolved referred to as the *Intermediate web*. The total number of links (L), species (S), linkage density or connectivity (L/S), and directed connectance (L/S^2) were determined for each web (Martinez, 1991), as were the proportions of *top* (T), *intermediate* (I) and *basal* (B) species following the definitions of Cohen and Briand (1984) and Briand and Cohen (1984).

The number of links between T, I and B compartments were determined for each web, and the mean chain length calculated as the total number of different chains in a web divided by sum length of all chains following Pimm (1982). Similarity of seasonal food web matrices and determination of trophic species was carried out using the similarity

index of Jaccard (following Schmid-Araya *et al.* 2002). Whilst predator-prey ratio for each web was calculated by dividing the total predatory species by the total prey species including cannibalism (Martinez, 1994) so that the data could be compared with other published, highly resolved webs.

Species of both meiofauna and macrofauna were also classified into functional feeding groups based on definitions of Cummins (1974). Designation to the functional feeding groups of Cummins (1974) was *a priori* based upon knowledge of the feeding biology of different taxa derived from taxonomic literature (see Appendix 1) and personal communications with Dr J. M. Schmid-Araya and Dr P. E. Schmid. Taxa for which there was any doubt *a priori* as to their functional feeding category were omitted from analyses. The frequency of occurrence of different food items in the gut for individuals belonging to the different functional feeding groups was then summed and divided by the total number of individuals examined over the whole year. Annual proportions for the different functional feeding groups were then compared.

Isotope samples

Twelve additional modified Hess samples, six from each of the macrophyte stands and gravel beds, were also taken at random in November and January 2004, as well as May through October 2005, for isotope analysis of meiofauna. Standard procedures outlined above were used for transporting the meiofauna isotope samples to the laboratory and treatment thereafter.

Stream detritus for isotopic sources analysis was obtained from the modified Hess samples used to collect meiofauna. From June 2005, tiles were placed within the macrophyte stands at random one month before obtaining 3 replicate samples of biofilm at each sampling occasion. Tiles were scraped with a plastic brush, washed with deionised

water, and any large invertebrates removed by eye from the resulting slurry. The slurry was then filtered onto pre-combusted and pre-weighed GF/C filters (diameter 25 mm, Whatman), each stored in a separate small plastic bag. Cuttings of the dominant macrophytes, *Ranunculus spp.* and *B. erecta* were also taken on each sampling period from June, each cutting being stored separately in a small plastic bag. All samples of isotopic source materials were kept cool during transport to the lab where they were frozen for later SIA preparation.

The reduced column for SIA

An ideal minimum tissue sample dry mass of ~0.8 mg is required for accurate determination of stable isotope ratios using most laboratory elemental analyser-stable isotope ratio mass spectrometer (EA-IRMS) systems. Work by S. Tod (unpublished) revealed that the mean dry weight of individual specimens of the dominant meiofauna taxa found in the River Lambourn would range from ~0.001 mg to ~0.02 mg. Between 50 and 1000 meiofauna individuals per replicate isotope sample were therefore required. Moreover, benthic meiofauna within the macrophyte stands are sediment associated and require significant searching time to accumulate large numbers of individuals. In order to overcome sample collection difficulties, a reduced column isotope analysis technique developed by Carman and Fry (2002) and Houghton *et al.* (2002) was used.

Standard EA-IRMS systems work by combusting samples in an oxidation column. Samples are then transported by a flow of helium through a reduction column which removes impurities and a water trap which dries them. Eventually samples reach the IRMS which analyses quantities of N and C, and stable isotope compositions ($\delta^{15}N$ and $\delta^{13}C$). Normal oxidation and reduction columns used in the EA are made from high quality quartz tubes, volume ~59,700 mm^3 (ID ~13mm, Height, ~450mm). In the modified method the

volume of both the oxidation and reduction columns was reduced to ~34,265 mm^3 (see Fig. 18 a). This has the effect of reducing the head space inside the columns, less helium is then required to transport gaseous samples from the EA to the IRMS. Consequently, gaseous samples become less dilute with helium during transport, the higher concentrations reaching the IRMS allowing for smaller tissue sample sizes to be used.

As an indication of the improved sensitivity of the EA-IRMS system at Queen Mary, with the reduced column an isotopic signature with a mass of N equal to approximately 2.5 μg with a standard EA (Flash EA, 1112 Series, Thermo-Finnigan, Bremen, Germany)-continuous flow IRMS (Delta Matt Plus, Thermo-Finnigan, Bremen, Germany) was obtainable. Whereas with a reduced column EA-IRMS system an isotopic signature was obtainable down to a mass of N equalling 1 μg. Tests of accuracy with 28 samples of urea over 12 different volumes of 0.0025 M ranging in mass from 1 to 5μg of N revealed a $\delta^{15}N$ mean of -1.41‰ (± 0.09 s.e.) (Fig. 18 b). Over the same urea volumes with a C mass of 1 to 2 μg a mean $\delta^{13}C$ of -43.58‰ (± 0.89 s.e.) was found (Fig. 18 b).

Carman and Fry (2002) discuss problems associated with functioning of EA-IRMS systems with small sample sizes, in particular the contamination of samples with atmospheric N, and trace C due to large tin cups. Contamination of C was avoided by using smaller tin cups as recommended by Carman and Fry (2002) reflected in the lack of $\delta^{13}C$ signatures for over twenty blank sample runs which were carried out (Fig. 18 b). The EA-IRMS system was also extremely clean reflected in the lack of $\delta^{15}N$ signatures found for blank samples. Blank correction was therefore not need for the SIA results.

Meiofauna and isotopic source SIA preparation

Meiofauna are capable of extremely high tissue turnover rates (Benke, 1998; Stead *et al.* 2005a; Reiss, 2006; Chapter 3), so to ensure stable isotope signatures of meiofauna were

real and not affected by conditions associated with sample storage a maximum of five day lab processing period was set. Samples were sieved and subsampled, meiofauna being hand sorted with a very fine pipette under a stereo microscope (25x/50x). Only the meiofaunal groups for which enough material could be collected for SIA were sorted, i.e. non-predatory chironomids, predatory chironomids, harpacticoids, nematodes and oligochaetes. Further taxonomic resolution of groups was not feasible as individuals need to be slide mounted for exact identification. Moreover, many of the individuals were juvenile and did not possess full diagnostic features for identification. It was decided that taking a representative sample of each group for species identification was too inaccurate as multiple species co-existed (Chapter 2; S. Tod unpublished for nematodes).

Meiofauna were thoroughly washed with deionised water and then left for 12 h to ensure gut evacuation. Individuals were then fixed by freezing so as to avoid tissue contamination, and placed directly into pre-weighed ultra light weight tin cups (size 4 x 3.2 mm: Elemental Microanalysis, UK) using fine forceps. Tin cups containing tissue samples were then dried at 60^0C for 6 h and reweighed to obtain sample weights. Approximately 5 chironomids, 3 predatory chironomids, 10 oligochaetes, 30 harpacticoids and 30 nematodes were needed per tin cup. A minimum of two and maximum of eight replicate tin cups was adopted per meiofauna group when enough material was found, except for Oligochaeta in winter (see Table 9).

All isotopic source samples were run under standard EA-IRMS conditions with pre-weighed tin capsules (size 8 × 5 mm: Elemental Microanalysis, UK). Sediment organic matter samples were dried at 60^0C and homogenised. Removal of live and dead meiofauna from sediment samples prior to SIA revealed no significant difference in isotope signatures (S. Tod. unpublished). Sediment samples were divided into two portions, the first being weighed into tin cups ready for SIA. The second portion underwent aqueous acidification

where 25-50 mg was preweighed into a glass vial and treated with 2.5 ml of organic free 1N HCL. Samples were then agitated in an ultrasonic bath and left for 12 h to dry at 50^0C. Dry samples were then left for 24 h to allow hydroscopic salts to equilibrate before being weighed into tin cups for SIA.

Filter papers containing biofilm samples were dried at 60°C for 24 h and then reweighed to obtain total sample biofilm weight. Biofilm samples were unacidified as no significant difference in δ^{13}C signatures was found with treatment (S.Tod, unpublished). A small core (diameter 5 mm) was taken from each filter paper and placed in a tin cup for SIA. Macrophytes were separated from epiphytic invertebrates and biofilm by shaking vigorously in 1 L of deionised water. Plant material was then checked for invertebrates and dried at 60°C before being homogenised, between 1 and 2 mg of the resulting powder being placed in each tin cup for SIA.

Three replicate tin cups were analysed per isotopic source per season and lab treatment type, except for sediment samples where nine were used. All samples were corrected against secondary standards (NIST, Gaithersburg, MD, USA); sucrose with a known relationship to Vienna PeeDee belemnite, and ammonium sulphate with a relationship to atmospheric nitrogen. Over 100 samples of an internal standard (cyclohexanone-2,4-dinitrophenylhydrazone, Thermo-Quest, Italy) used during the analytical period gave a precision of 0.14% for nitrogen and 0.13‰ for carbon.
A non-parametric Kruskal-Wallis test in Statistica (Statsoft, USA) was used to test for differences in the δ^{15}N and δ^{13}C estimates of the isotopic sources and most common meiofauna groups between seasons.

RESULTS

Patterns in web properties

In total, 177 different consumers and food resources were identified in the River Lambourn including 49 different diatoms, 12 other basal resources such as detritus, algae and leaf material, 3 types of invertebrate eggs, 112 invertebrates and 1 fish species (see Appendix 7). Jaccard similarity index revealed that all four seasonal webs were reasonably distinct from one another, the closest similarity of approximately 56% occurring between the autumn and winter webs (Fig. 19).

Web size ranged from 77 species in winter to 133 species in summer, the number of links and linkage density being directly proportional (Table 10). Directed connectance was low and constant across all seasons ranging between 0.042 and 0.046, whilst no more than two trophic species were found in any seasonal web, their impact being low even when web taxonomic resolution was reorganised (Table 10).

A high proportion of basal species ranging between 0.354 and 0.454, and intermediate species ranging between 0.481 and 0.560 were found each season, top species only ranging between 0.036 and 0.090 (Table 10). Meiofauna were much more abundant than macrofauna in each season (Fig. 20), which is consistent with there being a greater influence as intermediate taxa. The dominance of intermediate and basal species was reflected in the proportion of *I-B* links found in each seasons which never decreased below 0.794. Consistent with the rareness of predatory taxa, there was a low proportion of *T-I* and *T-B* links and also of predator/prey ratios (Table 10). Mean chain length was always low, with a maximum value of 1.89 being recorded for the summer web (Table 10).

The summer web (Fig. 21) demonstrated the typical trophic structure of the community throughout the year outlined by the web properties summary (Table 10); with there being a high number of basal and intermediate species, and a low number of predatory

taxa. The web also clearly shows the significant proportion of top consumers for which no predators could be found, and the low number of trophic levels which were reflected in the mean chain length calculations (Fig. 21).

Effects of resolution on the summer web

Poorly resolving basal or intermediate groups significantly reduced web size, and predictably changed proportions of the basal and intermediate species (Table 10). Interestingly 34 more links were lost from the *Basal web* than the *Intermediate web* even though 11 fewer species were lost. Directed connectance decreased in the *Basal web* and increased in the *Intermediate web*, while chain length remained roughly constant in the former and increased significantly in the latter. Within the *Basal web*, the proportion of *I-B* links decreased, with *I-I* and *T-I* links increasing (Table 10). Whereas in the *Intermediate web* the proportion of *I-B* links decreased significantly, the proportion of *T-B* links approximately doubling, and *T-I* and *I-I* links increasing slightly. In both webs, decreasing taxonomic resolution and effectively web size had a predictable effect of increasing the proportion of predators and consequently the predator-prey ratio.

Isotope analysis

Over the four seasons allochthonous sources of carbon with a $\delta^{13}C$ range of -31.32 to -30.97‰ were significantly less enriched than autochthonous sources which varied between -37.96 and -34.79 ‰ (Fig. 22). Of the isotopic sources only biofilm displayed significant seasonal changes most pronounced between $\delta^{15}N$ in spring and autumn (Kruskal-Wallis ANOVA, $P = 0.049$), and $\delta^{13}C$ between spring and summer (Kruskal-Wallis ANOVA, $P = 0.049$). *Berula erecta* maintained a consistently lighter $\delta^{15}N$ signature than biofilm and

Ranunculus sp. in each season (Fig. 22). Base line isotopic source data encompassed the range of meiofauna isotopic signatures in each season well (Fig. 22).

The mean mass per tin cup across all meiofauna samples was 2.26 μg (± 0.17 s.e.) for N, and 5.64 μg (± 0.44 s.e.) for C, both well above the lower limits required for accuracy in determining isotopic signatures outlined in the method (see Fig. 18 b). Error bars indicated some noticeable variation in $\delta^{13}C$ for each meiofauna group within seasons (Fig. 22). Significant and weak nearly significant variation in $\delta^{13}C$ signatures of the commonest meiofauna groups between seasons was also found (Kruskal-Wallis ANOVA: harpacticoids, $P = 0.084$; nematodes, $P = 0.029$; Non-predatory chironomids, $P = 0.005$). The position of most meiofaunal taxa between the range of autochthonous and allochthonous food sources in each season suggests a strong dependence on a mixed diet (Fig. 22).

No significant variation was found in the $\delta^{15}N$ signatures of non-predatory chironomids, harpacticoids and nematodes between seasons (Kruskal-Wallis ANOVA, $P > 0.100$). Applying the standard estimate of between 3-4‰ fractionation of $\delta^{15}N$ among trophic levels (Post, 2002), meiofauna do not even encompass one trophic level's worth of variation in $\delta^{15}N$ (Fig. 22). Furthermore across the whole community including basal resources the maximum number of trophic levels that can occur is estimated as between 1.75 and 2.33 (Fig. 22).

Functional feeding groups

A remarkably constant pattern was found when the frequency of occurrence of different food items across individuals within the different functional feeding groups was examined (Fig. 23). Detritus was the most frequently found food item occurring in more than half the individuals across all the different groups (Fig. 23). Diatoms were nearly as well

represented as detritus in each group except in shredders (Fig. 23). Stones and plant material were found in a proportion equal to or greater than 0.1 of all individuals examined in each group. Nearly half of all predator individuals (0.48) and a quarter of all shredder individuals (0.24) examined contained prey remains, and only a very small proportion of individuals in each group had empty guts (0.04-0.19).

DISCUSSION

Food webs for the chalk stream River Lambourn were some of the most speciose described for lotic environments. A significantly high number of intermediate taxa, mainly of meiofaunal size invertebrates and chironomids were present along with a large number of different diatoms. Changing taxonomic resolution significantly changed web properties. The modified SIA technique was able to distinguish seasonal and between species variation within the meiofauna. Along with gut content data, the SIA indicated neither a strong heterotrophic or autotrophic dominance of the food web, the River Lambourn fitting most congruently to the original RPM of Thorp and Delong (1994).

Web size, taxonomic resolution and seasonal variation

Various stream studies have reported food webs with between 31 and 113 species (Tavares-Cromar and Williams, 1996; Townsend *et al.* 1998; Closs and Lake, 1994). The web size of the Broadstone stream increased from 24 to 39 species (Hildrew *et al.* 1985; Woodward and Hildrew, 2001) up to 54 to 86 species when the meiofauna were included (Schmid-Araya *et al.* 2002a). Tavares-Cromar and Williams (1996) found web sizes between 31 and 39 species for one stream, but lumped together 159 different diatom species. The size range for the seasonal webs found in the River Lambourn of 77 to 133 species although high is

probably more accurate than some previous food web descriptions due to the greater taxonomic resolution of basal and meiofaunal species.

Closs and Lake (1994) and Warren (1989) have reported significant seasonal changes in food webs of freshwater systems. Schmid-Araya *et al.* (2002a) also found distinct seasonal changes with similarities in summer/autumn and winter/spring which reflected changes in species composition. They postulated variable flow, CPOM input, or invertebrate life histories for the observed pattern. Within the River Lambourn greatest similarity was found between the autumn and winter webs. The spring and summer food webs were much larger, probably due to the seasonal influx of new species around this time. Spring/summer coincides with an observed increase in density of the most speciose insect group in the River Lambourn, the Diptera family Chironomidae (Chapter 2). Moreover higher biomass, primary production, and species richness of diatoms has been found in some English chalk streams during spring and summer (Marker, 1976 a,b). Temporal changes in webs were therefore most likely driven by changes in species composition.

Highly resolved webs are often dominated in species number by intermediate taxa (Polis, 1991; Martinez, 1991; Hall and Raffaelli, 1991). Similarly, in the River Lambourn a high contribution of intermediate species to web size was found in each season, but in contrast to many published webs significant contributions of the basal species were also found reflecting the diversity of diatoms. Proportions of *T*, *B*, and *I* species, were sensitive to changes in taxonomic resolution as reported by Martinez (1992). A high number of intermediate species translated into a dominance of *I-I* links in webs of previous studies (Martinez, 1991; Goldwasser and Roughgarden, 1993). However, Schmid-Araya *et al.* (2002a) found an approximately even and high contribution of both *I-I* and *I-B* links in each season. Within the River Lambourn webs, *I-B* links were most dominant. The data do not

fit the generalisation of Havens (1992) that link proportions decrease from the base to the top of webs.

Unlike the Broadstone stream webs of Schmid-Araya *et al.* (2002a), autochthonous sources of carbon were frequently found. Despite this difference and other variations in web proportions, high resolution of taxa for seasonal webs within both streams resulted in around 4 links per species and decreased directed connectance of around 0.04-0.08. Schmid-Araya *et al.* (2002a) postulated low directed connectance was due to the high number of intermediate taxa observed. While, an examination of eleven webs derived from seven different streams found that directed connectance remains relatively constant with web sizes of greater than 70 species (Schmid-Araya *et al.* 2002b). The manipulations of taxonomic resolution for the *Basal web* resulted in directed connectance of 0.039, and for the *Intermediate web* of 0.056, suggesting that the proportion of intermediate taxa and not of web size *per se* predominantly determines directed connectance values.

Previous studies have advocated lumping taxa with close dietary overlap as "trophic species" (Briand, 1983; Martinez *et al.* 1999). However, the studies of Schmid-Araya *et al.* (2002a) and Winemiller (1990) with high resolution and low trophic overlap do not support this. No support for lumping species was found from the River Lambourn food webs as levels of trophic overlap were extremely low.

The number of predatory or omnivorous taxa (consuming animal prey and basal resources) was constantly low in all seasons and reflected in the low average chain lengths for each web. Moreover, a high number of top consumers were found which in combination with resolution of diatoms probably contributed to the high number of *I-B* links. The River Lambourn is known to contain large stocks of trout which have been shown to significantly reduce macroinvertebrate numbers in other streams (Rundle and Hildrew, 1992), and particularly those of large predatory taxa (Meissner and Muotka, 2006). Chalk streams also

contain significant numbers of ciliates (Baldock, 1983) and most likely other protists. Inclusion of these taxa may well have significantly changed web properties, in particular proportions of *I-I* and *T-I* links, possibly even directed connectance, and explain the number of top consumers which Polis (1991) describes as an artefact of insufficient sampling.

SIA and Functional feeding groups

Jardine *et al.* (2005) reported a high correlation between the isotopic signature of gut content and tissue from individual macroinvertebrates in streams. The level of taxonomic resolution in this study was coarse and changes in $\delta^{13}C$ signature of meiofauna groups between seasons may reflect changes in the species composition. However, a general pattern seemed apparent where meiofauna did not exclusively derive carbon from either allochthonous or autochthonous food sources. Grazing of bacteria, algae, detritus, diatoms, and protozoa by lotic benthic meiofauna has been documented (Perlmutter and Meyer, 1991; Borchardt and Bott; 1995; Bott and Borchardt, 1999; Hall and Meyer, 1998). A strong dependence of intermediate taxa including many meiofauna on detritus and autochthonous carbon sources was indicated by the gut contents analysis of meiofauna. Furthermore, the macroinvertebrate gut contents analysis indicated widespread generalist feeding, which was confirmed by the SIA of Pretty *et al.* (in press) where wide variation in $\delta^{13}C$ was observed for many macroinvertebrate taxa found within the River Lambourn.

A noticeable variation in the $\delta^{13}C$ of different meiofauna groups within seasons was found. Pretty *et al.* (in press) also found this pattern for separate species of macroinvertebrate in the River Lambourn using standard SIA. Consequently, the sometimes large individual variation in meiofauna $\delta^{13}C$ within seasons is probably not an artefact of either the coarse taxonomic level, or experimental methods used in this analysis. The

pattern probably reflects genuine variation between individuals of both macrofauna and meiofauna in consumption of food resources. In particular variation may be due to fluctuations in $\delta^{13}C$ of lotic algae consumed. Changes in algal $\delta^{13}C$ are known to be induced by variable flow (Finlay *et al.* 1999; Singer *et al.* 2005) a pattern also found in the River Lambourn (Pretty, pers. comm.).

A small variation in $\delta^{15}N$ between 4 and 8‰ was observed across the meiofauna community. Pretty *et al.* (in press) observed an almost identical variation in $\delta^{15}N$ of the macroinvertebrate taxa ranging from 4‰ to 9‰. This would imply the invertebrate food web only encompassed a maximum of around two trophic levels (Post, 2002) and thus, it is consistent with the average chain length calculations. However Pretty *et al.* (in press) revealed significant variation between seasons in the $\delta^{15}N$ of consumers who relied predominantly on autochthonous food sources. This implies fluctuations in $\delta^{15}N$ of the nitrogen sources available to autotrophs in the food web. Fluctuations would almost certainly mask variation between species feeding on multiple food resources. Furthermore, the gut content data revealed a high incidence of basal resources in the stomachs of predatory taxa within the River Lambourn, which would reduce $\delta^{15}N$ enrichment of predators relative to their prey confounding isotopic analysis of trophic structure.

Size and stage of decomposition are important factors in determining nutritional quality of detritus including C:N ratios (Moore *et al.* 2002), consequently larger particles may be more nutritionally valuable than small ones. Aquatic ecologists frequently divide detritus into size fractions of CPOM and FPOM which Cummins (1974) used to distinguish coarse particle feeders and fine particle feeders. The gut content data presented here revealed a significant presence of CPOM in some macrofauna such as *G. pulex*, and FPOM in some meiofauna such as the harpacticoids. However, despite feeding on different size fractions of detritus no clear separation in $\delta^{15}N$ values was found, even though invertebrate

groups showed low enrichment in $\delta^{13}C$ values suggestive of a mainly detritus based diet. This implies both size classes of invertebrate were feeding on the same food resources and detritus particle size was not important in understanding the food webs. This is possibly due to the high densities of shredder taxa such as *G. pulex* in the River Lambourn (Chapter, 2) which through sloppy feeding reduce the particle size of detrital material quickly before isotope signatures deteriorate, or because most of the nutritional quality of the detritus is in its bacterial content.

Fureder *et al.* (2003) reported a close correspondence between functional feeding groups, gut content, and stable isotope signatures. The SIA of Finlay (2001) indicated autochthonous carbon sources dominated stream communities at catchment size greater than 10 km^2, although variations corresponding to functional feeding groups did occur. Because of the meiofauna stable isotope results found in this study, it was decided that dividing micro and macro-consumers in the analysis of functional feeding groups was misleading. The functional groups gut content analysis strongly supported the generalist patterns indicated by the isotope data. A high degree of plasticity in the feeding was observed with both detritus and diatoms prevalent. As with some previous publications, a significant level of omnivory in predatory taxa, and predatory behaviour in macroinvertebrate shredder taxa was documented (Winterbourn, 1974; Feminella and Stewart, 1986; Malmqvist *et al.* 1991; Helms and Creed, 2005; Lancaster *et al.* 2005). No evidence supporting the lumping of taxa into "traditional" functional feeding groups was found, and with a catchment size at the field site well in excess of 10 km^2 with both diatoms and detritus forming important food sources the findings of Finlay (2001) had to be rejected.

Concluding remarks and a new simplified food web

Unlike in the headwater stream food web of Meyer (1994) the gut content and stable isotope data suggest discriminating between particle sizes of feeding for CPOM and FPOM is not essential, although some input to the FPOM feeders from shredders may be present (dotted arrow Fig. 24). The simplified food web diagram for the River Lambourn reflects the fact that meiofauna and macrofauna trophic positions and feeding are not easily separated. There is a noticeable generality of feeding across different functional groups, and size classes.

The data fit most accurately to the original RPM model proposed by Thorp and Delong (1994). An important caveat of this study is that inclusion of meiofauna may significantly change the heterotrophic-autotrophic balance of a system. Traditional studies of functional feeding, and river models/ concepts if refined with the inclusion of meiofauna could potentially be enhanced in their predictive capabilities and usefulness.

Table 9. The average number of individuals used per tin cup, number of replicate isotope samples used per season, and total number of meiofauna individuals used per season in parentheses for the stable isotope analyses performed on the River Lambourn.

Meiofaunal group	No. Ind.	Spring	Summer	Autumn	Winter
Chironomidae	5	8 (40)	5 (25)	7 (35)	3 (15)
Predatory Chironomidae	3			2 (6)	2 (6)
Harpacticoida	30	5 (150)	4 (120)	4 (120)	6 (180)
Nematoda	30	3 (90)	5 (150)	4 (120)	2 (60)
Oligochaeta	10	3 (30)			1 (10)

Table 10. Food web properties estimated for four seasonal webs, a summary web, and the two summer webs with variable basal and intermediate species taxonomic resolution from the benthos of the River Lambourn from spring, summer and autumn 2004, and winter 2005.

Property	Season Spring	Summer	Autumn	Winter	Summary	Summer *Basal*	Summer *Int.*
Web Size (*S*)	113	133	89	77	177	74	85
No. links (*L*)	540	817	361	266	1303	357	401
Linkage Density (*L/S*)	4.779	6.143	4.056	3.454	7.362	3.719	4.717
Directed Connectance	0.042	0.046	0.046	0.045	0.042	0.039	0.056
Mean chain length	1.720	1.890	1.230	1.630	2.245	1.849	2.177
Trophic Species							
Number	1	2	1	1	4	2	2
Trophic species size	(6)	(2) (2)	(4)	(5)	(12) (3) (3) (2)	(2) (2)	(2) (2)
Altered web size	108	131	86	73	161	72	83
Species proportions							
Basal	0.442	0.354	0.416	0.454	0.344	0.104	0.552
Intermediate	0.522	0.556	0.539	0.481	0.581	0.771	0.305
Top	0.036	0.090	0.045	0.065	0.075	0.125	0.143
Link proportions							
T-B	0.035	0.103	0.122	0.079	0.084	0.099	0.209
T-I	0.019	0.059	0.069	0.052	0.056	0.134	0.087
I-I	0.031	0.044	0.000	0.034	0.049	0.112	0.064
I-B	0.915	0.794	0.809	0.835	0.811	0.655	0.640
Predator/Prey	0.037	0.099	0.047	0.069	0.079	0.142	0.164

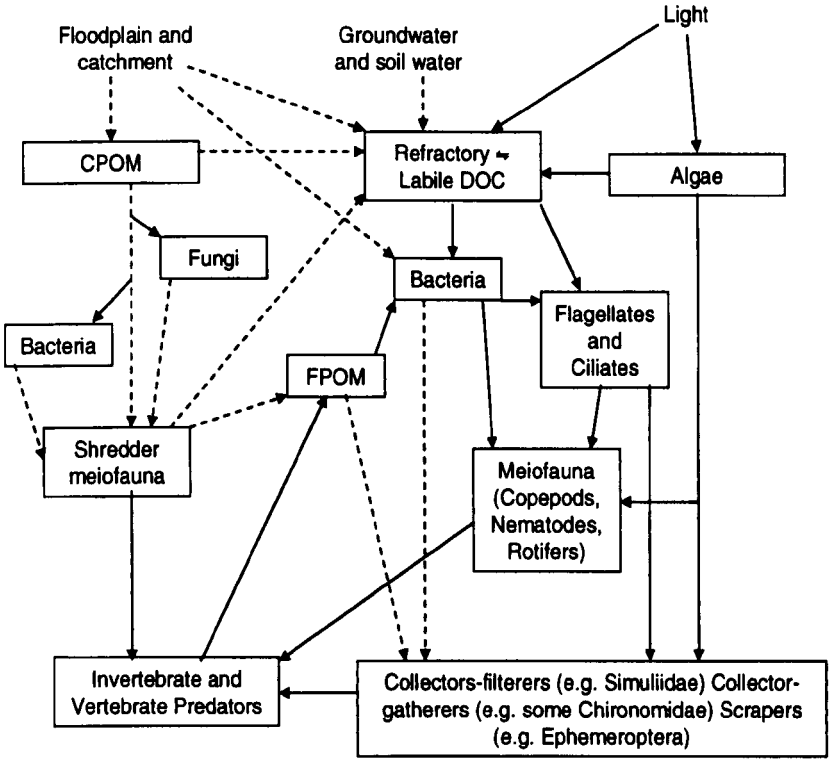

Figure 17. Diagram of a lotic food web displaying the major sources and pathways of organic carbon (adapted from Meyer, 1994). Dotted lines represent flows within the microbial loop not found in planktonic systems.

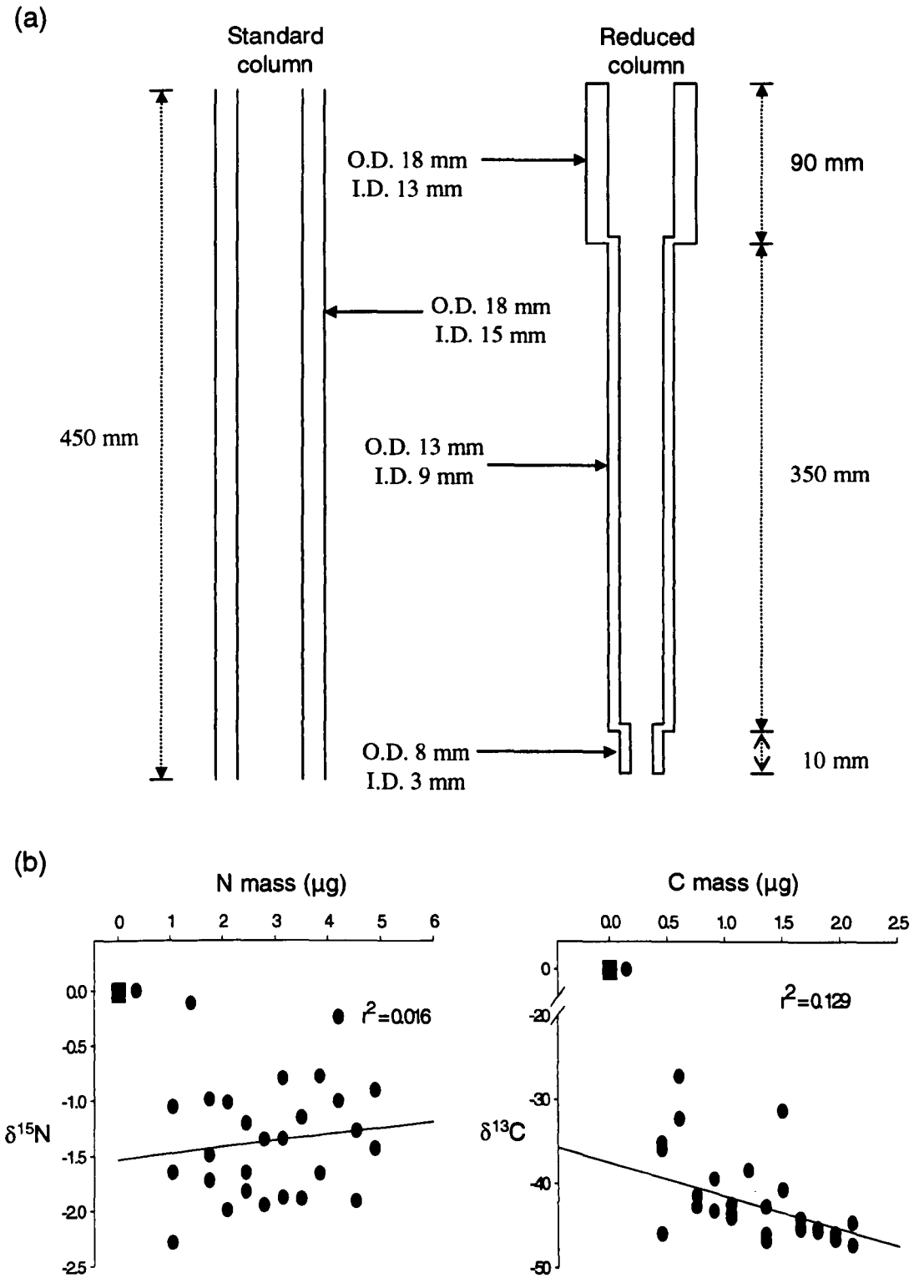

Figure 18. (a) Schematic diagram showing dimensions of the standard and reduced columns for the elemental analyzer, and (b) Uncorrected $\delta^{15}N$ and $\delta^{13}C$ values for samples with variable amounts of 0.0025 M Urea solution, blanks tin cups represented by squares all produced 0 values.

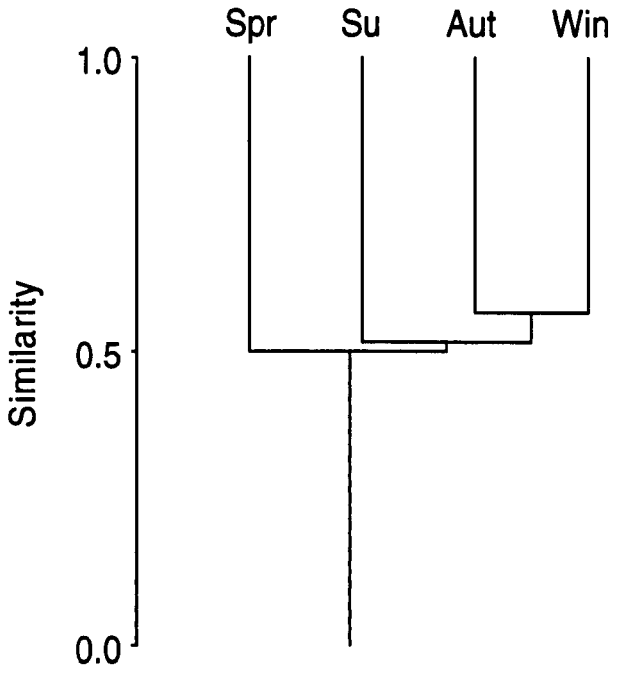

Figure 19. Seasonal food web trophic similarity based on Jaccard's similarity index (S_J) in the River Lambourn.

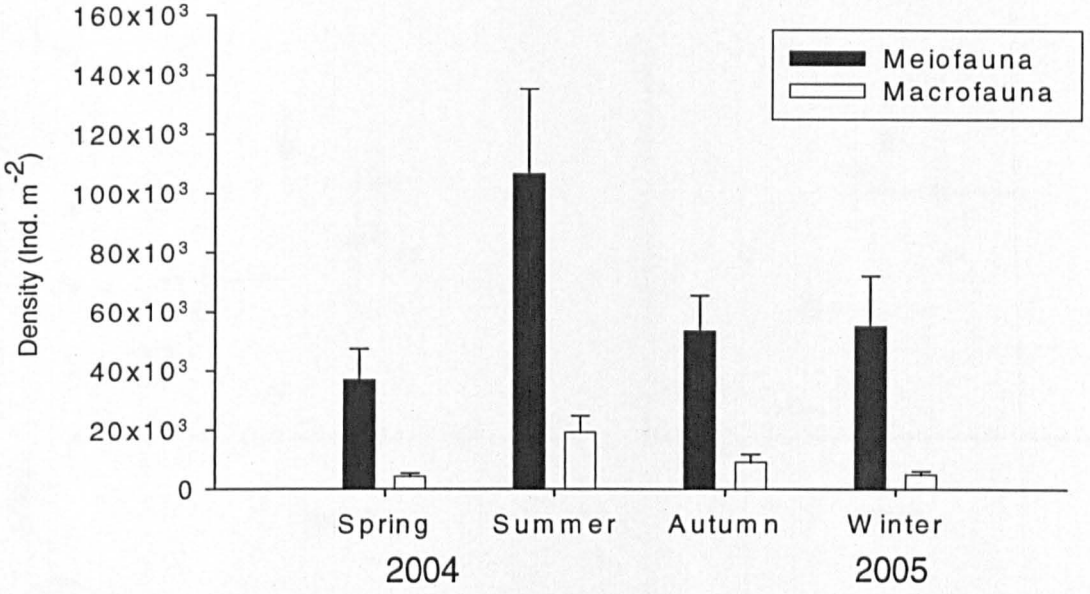

Figure 20. Mean (± S.E.) seasonal density of meiofauna and macrofauna in macrophyte stands of the River Lambourn.

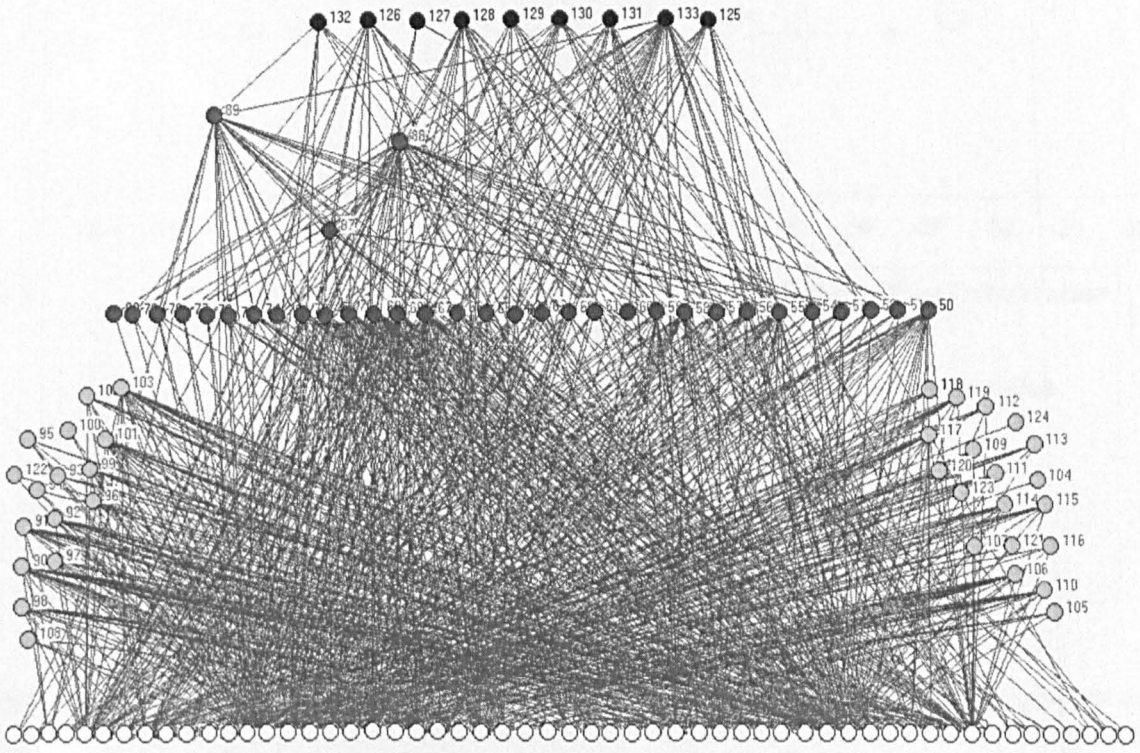

Figure 21. Invertebrate community food web of the River Lambourn for summer 2004. (Numbers are food items/species listed in Appendix 7; white circles, basal; light grey, top consumers; dark grey, intermediate; black, top predators)

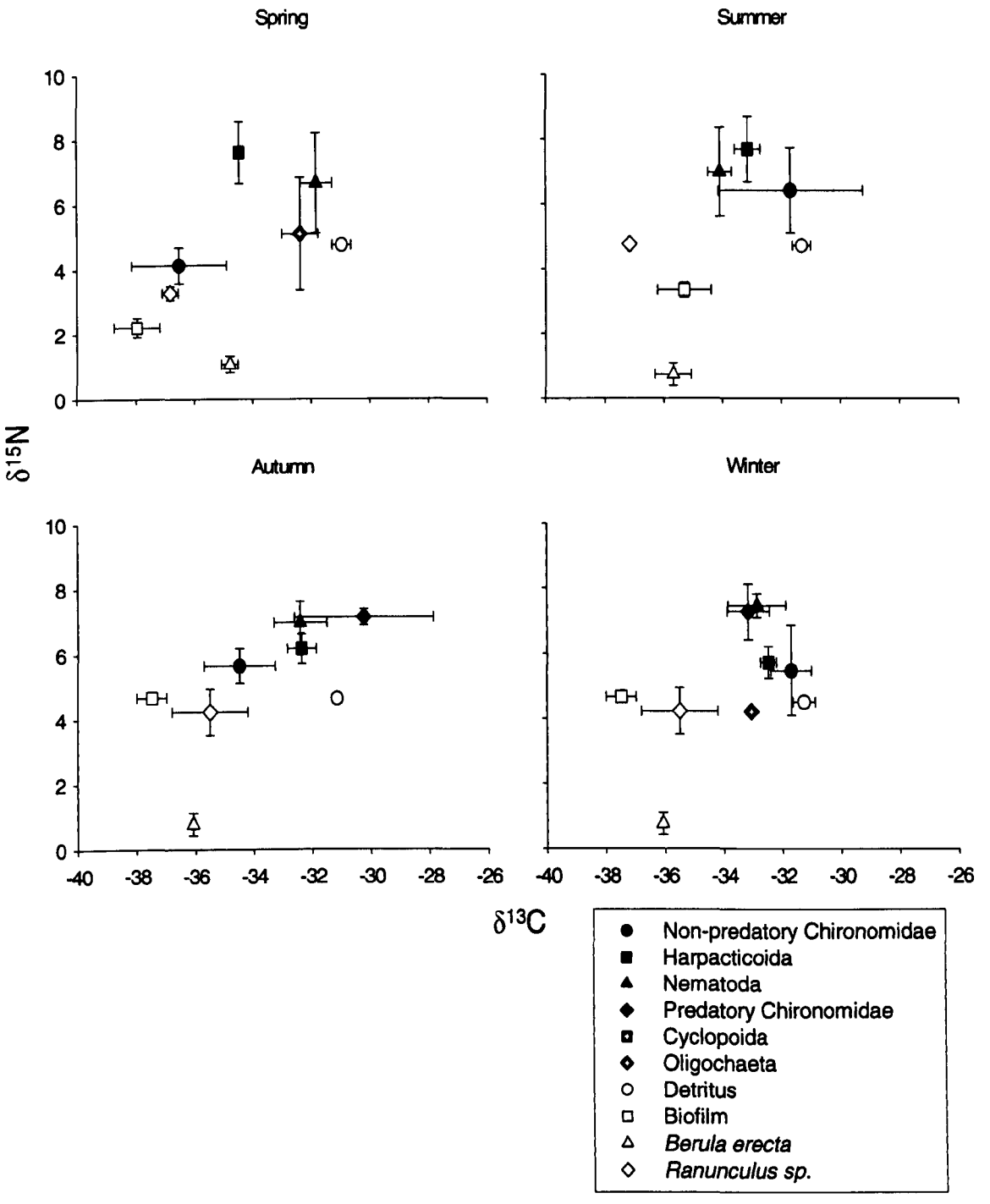

Figure 22. Mean (± 1S.E.) variation of $\delta^{13}C$ and $\delta^{15}N$ for various meiofaunal groups and their basal resources within the benthos of the River Lambourn during winter 2004, spring, summer and autumn 2005.

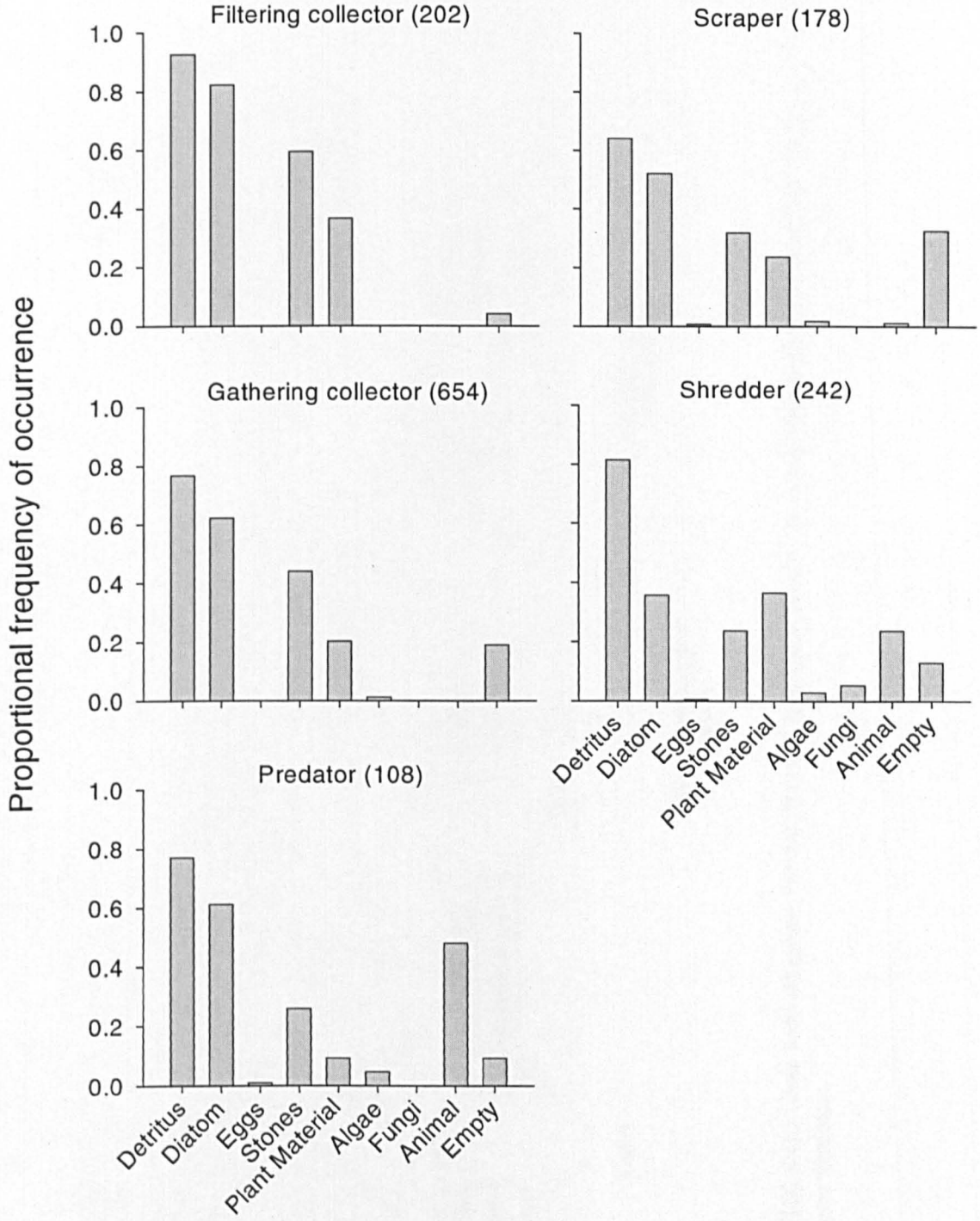

Figure 23. Frequency of occurrence of different food items within the guts of macrofaunal and meiofaunal individuals assigned to the main functional feeding groups as a proportion of the total number examined over the study period (indicated in parentheses) from within the River Lambourn.

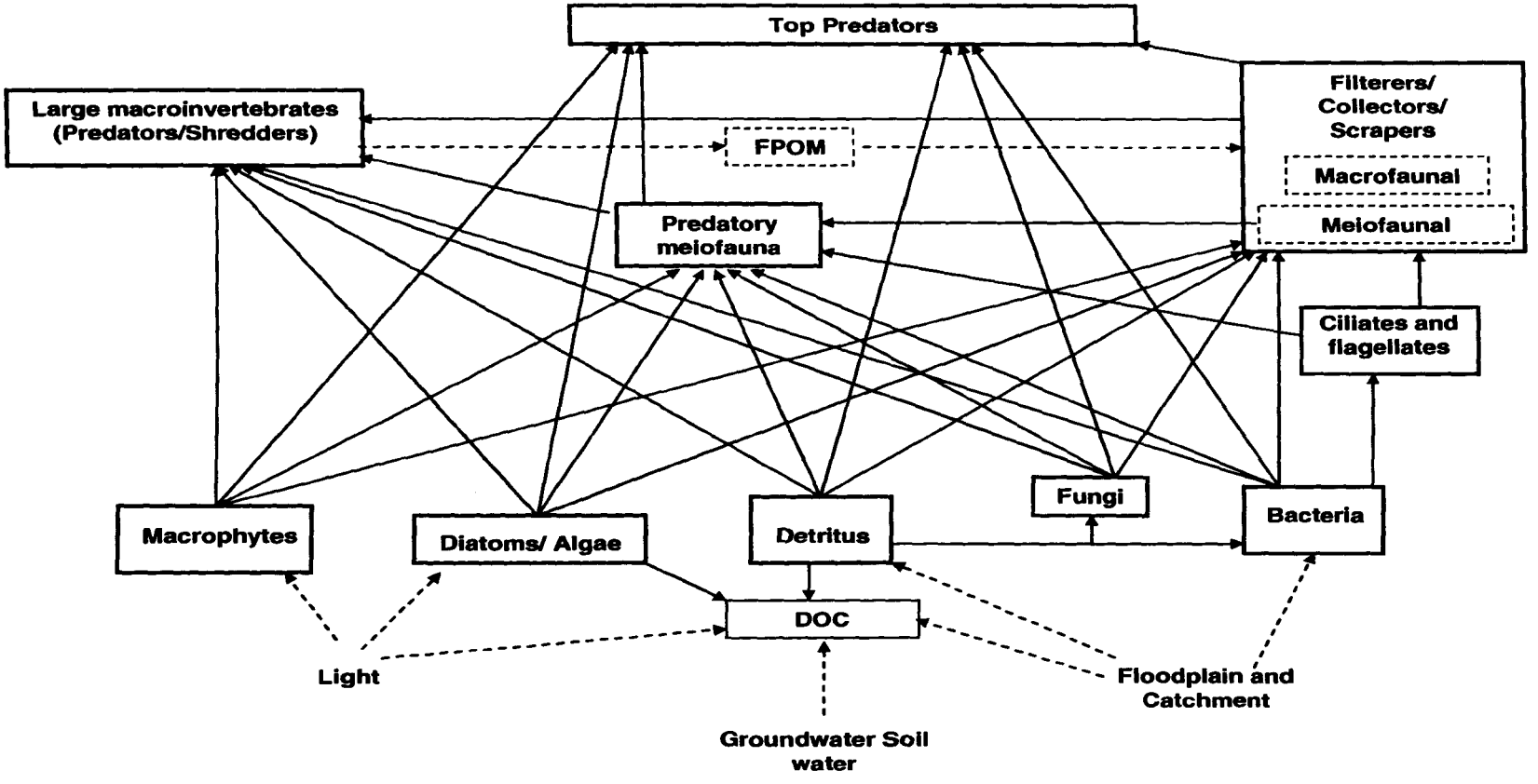

Figure 24. A revised simplified lotic food web diagram for the River Lambourn based on our findings and the original diagram of Meyer (1994) for headwater streams.

CHAPTER 5: ENERGETIC INEQUALITY LEADS TO STABILITY: DENSITY-BODY SIZE RELATIONSHIPS OF A CHALK STREAM INVERTEBRATE COMMUNITY

ABSTRACT

Within the diversity-stability debate of ecosystems there has been a synthesis between empirical and theoretical investigations of trophic interactions, structure and function. Investigations of energetics through allometric relationships of density have been largely ignored even though energy is a fundamental resource for all species. Energy is required for growth and, ultimately, persistence of species and may therefore determine interrelated ecosystem properties such as complexity, stability, and function.

Previously, a highly complex trophic structure and stable species composition was revealed for the benthic metazoan invertebrate community of a chalk stream. In this study the distribution of energy between individuals within this community is investigated through allometric relationships of density. Analyses of two benthic habitats, macrophyte stands and gravel beds, with a large body size spectrum extending over macrofauna and meiofauna are presented.

Temporally and spatially, constant bi-modal density-size spectra suggestive of a stable system were found. Peaks corresponded to meiofaunal and macrofaunal size classes possibly reflecting different modes of life. Density-body size distributions yielded shallower exponents than predicted from metabolic theory. Furthermore, the shallow exponents contrast with existing theoretical predictions that stable communities yield steep negative exponents. The data suggest stable systems may be characterised by no 'energy equivalence', and yield more positive exponents. Furthermore, the findings are consistent

with predictions of food web theory: that complex systems are characterised by many weak and few strong interactions. The many weak interactions were concentrated in smaller size classes at lower trophic levels. A greater functional redundancy in smaller size classes is possibly due to the influence of body size on food web structure, fractal geometry, and limits of the Lindeman efficiency on transfer of energy between trophic levels.

INTRODUCTION

The subject of stability in ecological systems is currently the focus of much attention (McCann, 2000; Ernest and Brown, 2001; Worm and Duffy, 2003; Makarieva *et al.* 2004) and is of great importance in light of the damaging anthropogenic effects currently occurring to natural communities. However the topic is not new, Odum (1953), MacArthur (1955) and Elton (1958) concluded that complex systems made up of many species are more stable than simple ones. These ideas were later challenged by theoretical and empirical work (May, 1973; Pimm and Lawton, 1978; Yodzis, 1981). However, more recent advances have reaffirmed the association of complexity with stability in communities (Johnson and Mann, 1988; Tilman, 1996; McGrady-Steed *et al.* 1997; McCann *et al.* 1998; Polis, 1998; Cottingham, 2001; Stachowicz *et al.* 2002; Romanuk *et al.* 2006). Furthermore, various investigations of different trophic groups and communities have found an association of higher species richness with improved ecosystem function (Hooper and Vitousek, 1997; Emerson *et al.* 2001; Loreau *et al.* 2001; Downing and Leibold, 2002; Duffy *et al.* 2003).

Determining causality in the relationships between diversity and stability, and diversity and productivity has proved elusive (Huston, 1997; McCann, 2000; Loreau *et al.* 2001). Worm and Duffy (2003) favour a synthetic theory of reciprocal relationships linking biodiversity with stability and productivity. Changes in biodiversity at the community level through bidirectional relationships can influence both stability and productivity of a system such as an ecosystem or community. Stability, influenced through disturbance events, affects biodiversity and, indirectly productivity of a system. Equally, productivity, through fluctuations in resource supply influences biodiversity and indirectly stability of a system. Worm and Duffy (2003) also postulate a bidirectional relationship between productivity and stability may exist.

Productivity can be limited by resource supply, consequently energy, a fundamental resource required for the maintenance of all biological systems from the cell, through individuals to communities, may influence diversity and stability of systems. The study of energetics through body size allometry has received considerable attention (Savage *et al.* 2004). This is in large part due to the predictions of metabolic theory that complex spatio-temporally variable structure and dynamics observed in ecological systems are largely a consequence of biological metabolism (Brown *et al.* 2004). Individuals of populations that shape structure and dynamics of communities and consequently ecosystems, require energy from metabolic activity for survival, growth, reproduction, and other processes such as ingestion and excretion (Peters, 1983; Brown *et al.* 2004). Basal metabolic rate (BMR) has been shown to scale to a 3/4 power with body size because of the presumed fractal nature of energetic pathways (West *et al.* 1997). Whilst the predominance of quarter power scaling (e.g. -3/4, -1/4, 1/4, 3/4) with body size of many different physiological variables from mammal heart rates to plant xylem flux rates has been taken as strong evidence for metabolic theory (Savage *et al.* 2004).

In an analysis of mammal species from a wide variety of habitats, Damuth (1981) found an inverse relationship between the log size of species and their log local abundance with an exponent of -3/4. Peters and Wassenberg (1983), extended the analysis to non-mammalian groups such as aquatic and terrestrial invertebrates and were unable to reject a -3/4 exponent, except for birds. Damuth (1981) argued that the exponent of density-body size and the 3/4 exponent of BMR effectively cancel one another, with no species gaining an energetic advantage due to size differences which became known as the 'energy equivalence rule' (Nee *et al.* 1999). Typically, where smaller species have a lower standing crop/biomass than larger ones their higher metabolic rates allow for faster individual

growth and population turnover compensating for the size difference (Damuth, 1981; Peters and Wassenberg, 1983).

Results of studies investigating species density-body size relationships since Damuth (1981) have been inconclusive. Marquet *et al.* (1990), investigating rocky intertidal taxa, and Schmid *et al.* (2000), examining two different stream invertebrate assemblages both found ordinary least square (OLS) regression slopes yielding exponents close to -3/4. However, more negative slopes rejecting the energy equivalence rule have been found in a number of aquatic communities (Cyr, 2000; Schmid *et al.* 2002). Meanwhile more positive relationships for birds and the invertebrate benthos of lakes have also been found (Brown and Maurer, 1986; Strayer, 1994), while no significant relationships dominated for tropical beetle, chironomid, and acid stream invertebrate assemblages (Morse *et al.* 1988; Tokeshi, 1990; Schmid, 2000; Stead *et al.* 2005).

The lack of conformity between studies towards the energetic equivalence rule has led various authors to seek alternative explanations for the density-body size relationship (Griffiths, 1998; Schmid *et al.* 2000,2002). The apparent polygonal pattern of variation in the density-body size relationship with some weak and strong negative slopes has been termed the 'constraint space' (Griffiths, 1998; Stead *et al.* 2005). Lawton (1990), suggested that the upper boundary of the constraint space may be limited by available energy, some evidence coming from a correlation of increased productivity with steeper slopes in lakes (Cyr *et al.* 1997). Consequently, the lower boundary could be constrained by sampling artefacts (Blackburn *et al.* 1993; Griffiths, 1998) or limits to the minimum viable population size (Silva and Downing, 1994).

In a recent theoretical explanation supported by empirical tests, Makarieva *et al.* (2004) suggested that fluctuations in the shape of the density-body size distribution may reflect changes in system stability. They argue that ecological communities are organised

such that they maintain stability through minimising fluctuations in crucial properties such as nutrient concentrations or the distribution of biomass between individuals. Consequently, in stable systems the share of energy going to larger heterotrophs should be suppressed. This is because large organisms have to move over greater areas to meet their energy requirements, in doing so they cause spatio-temporal fluctuations in resources such as organic matter and nutrients through concentrated deposits of their excreta. These biotic disturbances are predicted to disrupt communities from stable states.

Makarieva *et al.* (2004) predict that in unstable environments high fluctuations in abiotic variables may occur. When these fluctuations are too great to be controlled by the biota, restrictions on large heterotrophs are relaxed. This is because there is no gain to the community in terms of stability as biotically induced fluctuations are no longer significant due to the magnitude of the abiotic environmental fluctuations. Density-body size distributions in stable environments are predicted to be characterised by very negative scaling exponents and the opposite in unstable environments.

Another possible explanation for the variation in density-body size distributions may come from a synthesis with the size-spectra approach to studying body size patterns and in particular the work of Sheldon *et al.* (1972). When these workers investigated the size-spectra of particles in the oceans they found a roughly constant distribution of biomass across a range of body sizes in marine pelagic ecosystems. This implies a linear proportional decrease in biomass with size classes, now known as 'the linear biomass hypothesis' (Sheldon *et al.* 1986). Development of the hypothesis by Rinaldo *et al.* (2002) and Brown and Gillooly (2003) has led to the refinement of the 'energy equivalence rule'. Within trophic levels a hypothetical scaling value for density-body size allometry of -3/4 power is predicted as species share the same food sources. However, where species from multiple trophic levels are analysed together differences in body mass and trophic transfer

efficiency between levels must be taken into account, resulting in a scaling exponent of -1 (Marquet *et al.* 2005). Jennings and Mackinson (2003) have successfully applied the refined theory to a size-structured marine food web.

Even refining the energy equivalence rule, many of the published density-body size patterns would not conform to metabolic theory. Moreover, exceptions to the constant distribution pattern of biomass in size-spectra of marine and freshwater systems including 'step like' increases in biomass, uni-, bi-, tri- and multimodal size spectra contradicting Sheldon *et al.* (1972) have been published (see Stead *et al.* 2005). Schwinghamer (1981) and Warwick (1984) both found peaks in the density-size distribution of marine systems around the macrofaunal (retained on a 500 μm mesh) and the meiofaunal (retained on a 42 μm mesh) body sizes. Schwinghamer (1981) found a third peak around organisms belonging to microfaunal size, whilst Poff *et al.* (1993) found a trimodal spectrum, peaks corresponding to the sizes of meiofauna, macroinvertebrates and fish, in a stream.

Warwick (1984) hypothesised that bimodality was due to there being no intermediates between two different optima, each corresponding to a different combination of species traits related to body size. Whereas Schwinghamer (1981) suggested that the three modes he found in density-size spectra for marine benthic zones reflected the differences in the way individuals interact with or exploit their environment due to limitations of body size. Microfauna such as bacteria are small enough that they can colonise the smallest grain surface areas, the second size category would include interstitial dwellers, mainly meiofauna, whilst the final group consisting of macrofauna mainly burrow or live on the surface of benthic sediment (Schwinghamer, 1981).

Upon examination of abrupt shifts in density-body size relationships for North American mammals and birds, Holling (1992) argued that variable habitat architecture was a possible cause for differences in density-body size distributions found between studies

across different spatio-temporal scales. This leads to the hypothesis of Schwinghamer about the different modes and scales of life becoming testable. Substrata varying in dominant grain sizes from fine to coarse may alter in terms of interstitial pore spaces, available habitat for large and small size taxa, and consequently habitat architecture which might be expected to influence body-size spectra. Bourassa and Morin (1995) found no differences in the size spectra of invertebrate assemblages inhabiting streambed sediments of varying particle sizes. Marine studies of size spectra have not produced conclusive results either (Duplisea and Drgas, 1999; Parry *et al.* 1999; Duplisea, 2000). The only controlled experimental manipulation of substrate grain size using artificial sediment within a marine benthic habitat evidenced no effect of habitat architecture (Leaper *et al.* 2001).

However, Morse *et al.* (1985) demonstrated an effect of habitat complexity in terms of fractal geometry on terrestrial insect-plant communities, where more convoluted environments are predicted to support greater densities of individuals especially of smaller body size, thereby affecting density-size spectra. Further work on aquatic communities has demonstrated an effect of habitat complexity on taxon richness, density, biomass, biomass-body size scaling, and density-body size scaling (Jeffries, 1993; Gee and Warwick, 1994; Taniguchi and Tokeshi, 2004; McAbendroth *et al.* 2005). The most detailed study of stream communities by Schmid *et al.* (2002) predicted that invertebrates can use their habitat in a continuum of ways scaling with a fractal dimensions of $D \geq 1$. They demonstrated that the body size distribution of mainly insect taxa scaled with seasonal variations in habitat complexity estimated from fractal properties, and not energetic constraints.

In another attempt at explaining species body size distributions, May (1986) argued that, as linear dimension increases, the number of species of a given size decreases, with an exponent to mass of -2/3. This would imply that smaller species subdivide their habitat more finely than larger ones. Therefore, species richness should increase with decreasing

body size. However, Brown (1995) stated modal patterns of species richness often exhibit peaks at intermediate body size, while Schmid *et al.* (2000,2002) found significantly higher species richness of invertebrates in two streams at intermediate body size.

In Chapters 2, 3, and 4, the most detailed investigation yet of benthic meiofaunal and macrofaunal invertebrates inhabiting gravel beds and macrophyte stands of a chalk stream in southern England was presented. The invertebrate community of the benthos in the River Lambourn was found to be highly diverse, creating a complex community in terms of trophic interactions. Furthermore, significant differences in species richness, density, and biomass between benthic habitats with some seasonal fluctuations were observed, as well as differences in secondary productivity between benthic habitats.

The first objective in this chapter was to examine the form and possible variation of the monthly density-size spectra within and between the two benthic habitats. Then, annual species-body size distributions were constructed to investigate whether the prediction of May (1986) that species richness increases with decreasing body size holds. Tests to determine whether seasonal and between habitat differences in density-body size relationships occurred are performed. Along with an examination of goodness of fit to any of the hypothetical scaling values of -3/4, -2/3 and -1 for metabolic, surface-area to volume and habitat complexity constraints on the community were carried out using Ordinary Least Squares (OLS) regression, and -1 for metabolic constraints using the Reduced Major Axis (RMA) regression methods which allows for greater variance in estimation of x and y axes.

MATERIALS AND METHODS

Study area

The study area was an 80 m reach of the River Lambourn as it passes through Bagnor near Newbury in Southern England, UK (51°25'29"N, 1°21'08"E). The river is groundwater fed,

draining a Cretaceous chalk catchment strongly affected by arable land farming, consequently the river is hypernutrified (Pretty *et al.* 2006) with a typical pH of around 7-8 (Chapter 2). Surface water temperature over the study period ranged between 7 and 15°C. The river has a channel width between 3 and 6 m, and a maximum water depth of 0.4 m (May 2004). Riparian vegetation immediately adjacent to the stream consisted of wetland on one side, and Salix *spp.* woodland on the other. The stable discharge and shallow slope in the study area of the River Lambourn characteristic of chalk streams (see Chapter 2), produced no well defined riffle-pool sequence on the streambed and the main heterogeneity was caused by structural features such as discontinuous growth of lotic macrophyte stands made up of *Ranunculus spp.*, *Berula erecta* (Hudson) Coville, and *Callitriche spp.*

Sampling

Quantitative benthic samples of the whole metazoan community (>42 μm) were taken monthly from April 2004 until March 2005. A modified Hess sampler (surface area: 2.71 dm^2; mesh size 42 μm) effective to a 5 cm depth into the chalk-stream substrate was used to sample the sediment surface-layer and macrophyte stands. Growth and recession of the macrophyte stands occurred unpredictably throughout the sampling period, and consequently, the area of exposed gravel beds varied. A fixed sampling design was used with twelve 2 m x 6 m sampling areas spaced at 7 m intervals along a longitudinal gradient of the stream channel so that the base line survey data could be incorporated into an investigation of surface-subsurface exchange in chalk streams (see Pretty *et al.* 2006). One Hess sample was then taken at random from within each sampling area with habitat type of each sample recorded. In total 138 Hess samples were taken due to difficulties with sampling apparatus in June (7 samples) and July (11 samples), in total 76 samples were taken from gravel beds and 62 from macrophyte stands.

Hess samples were kept cool (<10°C) during transport to the lab. The macrofauna and meiofauna fractions were then separated by passing samples through a 500 μm and 42 μm mesh sieves. All meiofaunal fractions (<500 μm) were kept refrigerated (<7°C) and sorted live to ensure soft-bodied taxa were accounted for. Macrofauna fractions (>500 μm) were preserved in ethanol and sorted after the meiofauna. During enumeration and counting, individuals were measured to the nearest micrometer using either an Olympus BX50 (Olympus Optical, Tokyo, Japan) (1250x magnification) microscope, or a dissecting microscope (25-250x magnification), except for soft-bodied meiofauna, Chironomidae and all Oligochaeta. Soft-bodied meiofauna were measured to the nearest micrometer using the Olympus BX50 and later identified where possible to species from film recorded with 3CCD JVC video camera (JVC, Tokyo, Japan), which was connected to the microscope. Chironomidae and Oligochaeta were measured using the dissecting microscope and then fixed on slides in Euparal for identification. Some abundant species (>30 individuals found in all samples from a substrate type in one month) were randomly subsampled and measured until a size frequency distribution approximating a 10% sampling error of the mean was achieved (Elliot, 1977). All measurements were then converted to dry mass using published body length/ biovolume regressions and conversion factors summarised in Chapter 2 where detailed descriptions of the sampling design, sample processing, taxonomic designations and body mass calculations can be found.

Statistical analyses and construction of size distributions

Population densities were converted to individuals per square metre to standardise units used in analyses. Data from each individual sample were then sorted into 25 body size classes of 0.3 log dry weight (μg) (P.E. Schmid, pers. comm.) and size class density data $\log_{10}$ transformed. Gaussian kernel density estimations and iterated searches for critical

band widths were performed on size distributions of gravel bed and macrophyte stand samples for each sampling occasion using the pre-release software, *EcoStatistics* (Schmid *et al.* 2002). The gaussian kernel density estimation analyzes multimodality of samples by smoothing data, enabling the identification of the position, magnitude and frequency of modes where this information would be lost if replicates were combined into mean size distributions (Stead *et al.* 2005). Within the method iterated (repeated) searches of data are carried out to find the closest match between data points to a Gaussian distribution. The measure of fit and level of rejection between different searches is set by a critical band width, effectively a level beyond which any pattern in the data cannot be differentiated from statistical noise.

Log annual species richness- log body size distributions were constructed for each habitat to determine the distribution of species richness along the body size spectrum. Density and body size data were then log transformed and OLS regressions performed seasonally and annually using Statistica (Statsoft Inc. USA). Seasonal and annual OLS regressions of density for the two benthic habitats were tested for fit to the hypothetical scaling values of -2/3, -3/4 and -1 with *t*-tests where:

$$t - statistic = \frac{(b - EXP)}{S.E._b}$$

Where b is the density body size exponent and EXP is the theoretically expected value.

Slopes and intercepts of seasonal density-body size distributions between and within the two habitats were then compared using multivariate analysis of covariance (MANCOVA). Finally, RMA regressions were performed on the density-body size distribution to check for an energy equivalence exponent of -1 using RMA v.1.17 (A. J. Bohonak, San Diego State University). This regression method is less sensitive to error in measurements of x and y variables than OLS particularly when low correlation coefficients

are found, and is superior when samples are taken from naturally polymodal distributions (Griffiths, 1998).

RESULTS

Density-size spectra

Kernel density analysis of macrophyte stand and gravel bed samples revealed a strong bimodal pattern in both habitats which was fairly constant between months (Tables 11,12; Fig. 25). Closer inspection of the magnitude and position of individual peaks across different samples in all months for both habitats revealed a remarkably constant pattern (Tables 11,12; Fig. 25). A peak was regularly found located at a log dry mass value of between -2 and -1 (0.01 to 0.1 μg dry wt) corresponding to meiofauna, and another less well defined secondary peak at log dry mass values of between 2 and 4 (100 to 10,000 μg dry wt) corresponding to macrofauna.

Species richness-body size patterns

Annual species richness-body size distributions showed a peaked pattern within the macrophyte stand habitat with most species distributed around an individual dry mass of 100 μg equivalent to a log dry mass of 2 (Fig. 26). In the gravel beds no obvious peak was found in the annual species richness-body size distribution, however more species were found across a range between 0 and 2 log dry mass (μg) (Fig. 26).

Species density allometry

Despite the contrasting patterns of peak species richness and a trough in density at intermediate body size, no pronounced peaked or polygonal pattern was found in any of the density-body size relationships (Table 13; Fig. 27). All annual and seasonal density-body

size OLS regression were statistically significant (P <0.01). Body size explained a significant amount of the variation in species density for the whole invertebrate community of the macrophyte stands (F = 222.86; df = 1,123; P = <0.001), and the gravel beds (F = 101.95; df = 1,94; P = <0.001). Exponents for the density-size distributions in the macrophyte stands ranged between -0.450 and -0.371, and in the gravel beds between -0.411 and -0.348 (Table 13). None of the hypothetical scaling values of -2/3, -3/4 or -1 fitted any of the OLS regressions (t-test, P > 0.05) (Table 13). Intercept values in the macrophyte stands changed from 2.820 and 2.927 in the spring and summer to 3.022 and 3.132 in the autumn and winter (Table 13). While in the gravel beds they remained low across all seasons ranging between 2.870 and 2.930 (Table 13).

RMA regression slopes were all steeper than the corresponding OLS slopes (Table 14). Within the macrophyte stands, RMA slopes ranged between -0.545 and -0.490, whilst in the gravel beds values between -0.503 and -0.469 (Table 14). Consistent with the OLS analysis, none of the RMA slopes yielded exponents close to -1 which would conform to metabolic theory (Table 14).

ANCOVA analyses revealed no significant effect of habitat or season on the slopes of density-body size distributions (Table 15).

DISCUSSION

In the chalk stream River Lambourn density-size spectra for both macrophyte stands and gravel beds showed a strong bimodal distribution which was stable temporally. A clear pattern of higher species richness towards intermediate body sizes was found. Density-body size distributions for both habitats were significantly shallower than those predicted through metabolic constraints. Similar to size-spectra, density-body size slopes remained stable between habitats and seasons.

Density-size spectra

Conformity between methods used to construct size distributions has been argued for by Ramsay *et al.* (1997) so that meaningful comparisons not confounded by methodological differences can be made across studies. Leaper *et al.* (2001) highlighted that in many marine studies, troughs such as the ones reported by Schwinghamer (1981) and Warwick (1984) might be sampling artefacts of the way macrofauna and meiofauna have been collected with separate pieces of equipment which operate on different spatial scales, necessitating extrapolation of density estimates to create size spectra.

Leaper *et al.* (2001) found a high variability in the number and position of modes in density-size spectra of benthic estuarine invertebrates in a study, where macro- and meiofauna were collected using a standard corer, thereby rejecting the hypothesis of Schwinghamer (1981). Moreover, Stead *et al.* (2005) also found a highly variable pattern for benthic invertebrates within an acid stream, where a modified Hess sampler was used to collect macro- and meiofauna simultaneously. In contrast, other studies have not found strong evidence for a bimodal distribution characterised by a trough between macrofaunal and meiofaunal size classes (Strayer, 1986; Ramsay; 1997; Duplisea, 2000). However, support has come from Poff *et al.* (1993) who found a trimodal distribution of body sizes in streams corresponding to meiofauna, macrofauna and fish species. Evidence for bimodality has also been found in some marine and freshwater studies (Gerlach *et al.* 1985; Raffaelli *et al.* 2000; Schmid *et al.* 2002).

The same modified Hess sampler technique for simultaneous sampling of meiofauna and macrofauna as Stead *et al.* (2005b) was used here. The technique was sensitive enough to detect synchronised seasonal and spatial fluctuations in the density of both macrofauna and meiofauna (Chapter 2), which suggests the sampling methods were appropriate to target an investigation of both size classes of invertebrate together. The data

presented here clearly demonstrate a strong bimodal distribution with a trough between meiofaunal and macrofaunal size classes supporting the hypothesis of Schwinghamer (1981).

Investigations of differences in density-size spectra across different habitats and grain size have been inconclusive in supporting or rejecting the hypotheses of Schwinghamer (Bourassa and Morin, 1995; Ramsay *et al.* 1997; Duplisea and Drgas, 1999; Parry *et al.* 1999; Duplisea, 2000; Solimini *et al.* 2001). Notably Poff *et al.* (1993) reported a difference between sandy substrates which are bimodal and macrophyte stands which are unimodal within Goose Creek. In contrast, within the River Lambourn both gravel bed and macrophyte stands habitats showed the same strong bimodal distributions.

Temporal variability of size-spectra and species-size distributions

Few studies have examined temporal variation in density-size spectra (but see Schmid *et al.* 2002; Stead *et al.* 2005). Stead *et al.* (2005) found large variations in density-size spectra between months using kernel density function analysis. They also found a high variation in the number of modes, their magnitude, and the position along the body size spectrum, between months. In contrast, one of the most striking features of the density-size spectra for the River Lambourn is the apparent lack of temporal variation from a bimodal distribution between months in both habitats.

Morin *et al.* (1995) and Solomini *et al.* (2001) have also reported stable density-size spectra. Morin *et al.* (1995) concluded that the average distributions of size spectra vary little among months even when recruitment of small organisms occurs. In the River Lambourn during the summer months within the macrophyte stands when the most significant changes in density, biomass and species richness of invertebrates was occurring (Chapter 2), examination of density-spectra showed no variation from bimodality in any

sample. We can therefore conclude that density-size spectra are stable in the River Lambourn and recruitment of all invertebrates, not just small taxa as proposed by Morin *et al.* (1995), exert a low impact on size distributions.

Species-size distributions

Warwick (1984) hypothesised peaks in density-size spectra were due to higher numbers of species congregating at certain points along the body size spectrum in communities. However, Schmid *et al.* (2002) reported seasonally stable patterns of higher species richness around intermediate body size classes in two separate streams, one with a bimodal and the other with a unimodal distribution. Within macrophyte stands and gravel beds of the River Lambourn a similar pattern was found with the highest number of species found around intermediate body sizes. In contrast, as we have seen, density-size spectra in the River Lambourn were strongly bimodal. Like Schmid *et al.* (2000,2002), I therefore have to reject the hypothesis of Warwick (1984) for the invertebrate assemblages of the River Lambourn, that declining densities are caused by a declining number of species at certain body sizes.

Like Schmid *et al.* (2000,2002) I cannot attribute the inverse scaling relationship of density-body size allometry found in the River Lambourn to a corresponding decline in the number of species hypothesised by Blackburn *et al.* (1993), as a central tendency for the species-size distributions was evident. Schmid *et al.* (2002) are probably correct in postulating that central tendencies for species-size spectra in streams probably reflect the lower number of taxa which can potentially occupy extremes of the body size spectrum; nearly all phyletic groups have species found in intermediate size classes.

Density-size distributions and competing hypotheses

Leaper *et al.* (2001) found no evidence for the habitat architecture hypothesis in their experimental manipulation of grain size, whilst various freshwater and marine studies have found no effect of sediment grain size on size spectra (Bourassa and Morin, 1995; Duplisea and Drgas, 1999; Parry *et al.* 1999; Duplisea, 2000). In contrast, through measurement of fractal dimensions Schmid *et al.* (2002) linked density-size distributions of mainly insect taxa to seasonal variations in benthic habitat complexity. Whilst, McAbendroth *et al.* (2005) used fractal analysis to demonstrate how higher habitat complexity supports greater invertebrate biomass, especially of small animals, resulting in differences between biomass-body size allometry of lentic macrophytes.

Within the River Lambourn, differences in habitat complexity would have almost certainly occurred between gravel beds and macrophyte stands due to the introduction of plant architecture (Morse *et al.* 1985), and increased sedimentation rates (White & Hendricks, 2000). Increases in habitat complexity may have also occurred in the macrophyte stands during spring-summer, the peak growing seasons of macrophytes (Ham *et al.* 1982), as new plant architecture grows potentially further increasing sedimentation rates. Moreover, as mentioned earlier, significantly higher density and biomass of the whole invertebrate assemblage was observed in the macrophyte stands and peak values were found in summer months (Chapter 2).

Despite potential changes in the habitat complexity and observed fluctuation in density and biomass of the invertebrate assemblage, density-size distributions followed a similar pattern to size spectra. No significant variation seasonally or between habitats in slope values was observed. Moreover, none of the OLS slopes values were close to or steeper than -1 which would indicate a possible influence of habitat complexity on density-body size allometry and support for the habitat architecture hypothesis of Holling (1992).

Interestingly though, seasonal differences were found between the intercepts of density-body size distributions within the macrophyte stands where significant changes in density and biomass took place, but not in the gravel beds where none took place (Chapter 2). This suggests meiofauna and macrofauna densities are stable relative to one another and co-vary. Evidence for co-variation in the seasonally synchronised fluctuation of density and biomass of both meiofauna and macrofauna in the macrophyte stands of the River Lambourn was found (Chapter 2).

Examination of density-body size exponents from OLS regressions demonstrated no clear fit to the -2/3, -3/4, or revised -1 hypothetical value. Whilst reduced major axis regressions also revealed scaling values significantly different from -1. Brown *et al.* (2004) stated that metabolic theory on its own cannot explain all variation in natural communities, residual variation caused by factors such as anthropogenic or natural disturbance events may also occur. As we have already detailed many documented deviations from the -3/4 exponent exist for aquatic systems (Tokeshi, 1990; Strayer, 1994; Cyr, 2000; Schmid *et al.* 2002; Stead *et al.* 2005), and the constraint space theory emerged as an explanation for exceptions (Lawton, 1990; Brown, 1995).

In their theory of the relationships between stability and density-body size distributions Makarieva *et al.* (2004) describe streams as particularly problematic habitats. They predicted the overriding impact of physical factors and high disturbance typically results in shallow *b* relationships for stream communities leading to a lack of conformance with exponents predicted by metabolic theory. Some independent evidence from the work of Cyr *et al.* (1997) has been published where shallower *b* relationships in lakes subjected to increased anthropogenic effects was found. Furthermore, Stead *et al.* (2005) found no relationship between density and body size in an acid stream where density-size spectra

revealed a highly variable pattern and high seasonal fluctuations in pH were known to occur.

However, as already discussed chalk streams provide typically stable environments for invertebrate communities in terms of flow and thermal regime. Moreover, previous analyses of species-abundance distributions for both benthic habitats of the River Lambourn suggested that the invertebrate assemblages were at equilibrium and probably subject to low levels of disturbance (Chapter 2). Additionally, examination of the seasonal fluctuations in density and biomass revealed only a few species or groups of taxa to be responsible for these changes (Chapter 2). Species composition of the assemblages varied little throughout the year. Combining these observations with the stable density-size spectra temporally and between habitats strongly suggests the benthic invertebrate communities of the River Lambourn were stable despite yielding shallow density-body size exponents.

Further evidence for stability of the invertebrate assemblages, which could explain the density-body size distributions patterns, comes from synthesis between the diversity-stability debate and food web theory. Investigations have revealed real food webs to be highly complex (Polis, 1991; Goldwasser and Roughgarden, 1993; Schmid-Araya *et al.* 2002) and also characterised by many weak and few strong interactions (Paine, 1992; McCann *et al.* 1998; Worm and Duffy, 2003). Furthermore Romanuk *et al.* (2006) showed that population stability of invertebrate species inhabiting rock pools with wider diet breadth measured through variability in stable carbon isotope values had lower fluctuations in density than species with narrow diet breadth. Effectively the hypothesis of MacArthur (1955) was proved where species which are able to rely upon a pool of multiple resources, dampen the impact of loosing one resource through feeding on others.

Predictions about communities can be made through the findings outlined above. Firstly, stable communities are likely to be diverse. This is certainly true of the River

Lambourn where 186 different taxonomic groups, mostly species, were identified from the survey of the benthos between April 2004 and March 2005 (Chapter 2). Secondly, stable communities are likely to be complex. This was confirmed for the River Lambourn invertebrate community through the highly taxonomically resolved benthic food web presented in Chapter 3. These ranged between 77 and 133 total consumers plus resources over four seasons and were some of the largest published stream food webs. Thirdly, stable systems should be dominated by weak interactions and generalist feeding. Strong evidence for this was found in the observation only a few species and taxonomic groups dominated density, biomass, and production, despite the high complexity of the system. Furthermore, a generalist feeding pattern was reported for all size classes of invertebrate (Chapters 2,3).

If stable communities are characterised by few strong interactions and a large number of weak interactions these may be significantly linked to allometric relationships. This is because the few strong interactions must involve compartments and flow paths in food webs which store and transfer proportionally much larger amounts of energy than those involving weak interactions. Differences in energy supply and storage through interaction strengths will affect population densities and biomass of species. The result should be the existence of a few dominant keystone species 'strong interactors' (see Paine, 1992; Woodward *et al.* 2005), a high number of species occurring at low density and biomass 'weak interactors', and, crucially, no energetic equivalence of stable communities. One important corollary is that this is only testable in 'real' ecological communities where density-body distributions are constructed from sampling of invertebrate assemblages which has taken place over an appropriate spatio-temporal scale to maintain potential effects of trophic-dynamics, diversity and stability.

Fractal geometry, the Lindeman efficiency and body size may further determine allometric relationships, whether species are strong or weak interactors within

communities, and the body size distribution of functional redundancy. Fractal geometry predicts that over the same surface area, resources such as space and food are more likely to be limiting for larger taxa of the same size than smaller ones (Morse, *et al.* 1985; Schmid, 2000). While the 'Lindeman efficiency' states that due to trophic transfer inefficiency, the amount of energy made available to higher trophic levels is always limited by that made available to lower trophic levels (Brown *et al.* 2004) and body size typically increases with trophic level (Warren and Lawton, 2004; Woodward *et al.* 2005; Jennings *et al.* 2007). Consequently, greater limitation on resources within higher trophic levels or larger body size classes should occur resulting in lower densities, functional redundancy, and species richness. In turn, this could facilitate the pattern of shallow density-body size exponents in stable communities such as those found in the River Lambourn.

Currently, there are no detailed studies of food webs, ecosystem dynamics, and body size allometry from within a single system which can test the predictions outlined here about the diversity-stability/density-body size relationship. However, basal and intermediate species were found in greater proportions in the River Lambourn food webs than top species, and as we have discussed all size classes showed generalist feeding (Chaper 4), which suggests greater functional redundancy at lower trophic levels. Furthermore, binary food webs do seem to take a triangular shape with more species in lower trophic levels suggestive of functional redundancy (Schmid-Araya *et al.* 2002; Woodward *et al.* 2005).

Concluding remarks

Density-size spectra displayed strong bimodal distributions within the River Lambourn consistent with the hypothesis of Schwinghamer (1981) about different modes of life such as interstitial dwellers and epibenthic burrowers. Moreover, central tendencies in species

richness along the body size spectrum appear to exclude the evolutionary hypothesis of Warwick (1984) for explaining the bimodal distribution. Density-size spectra were stable spatially and temporally and OLS regressions excluded the -1 scaling value. No conformance to any other hypothetical scaling relationship such as the -3/4 of energy equivalence was found.

The combination of observed density-size spectra, published findings of an investigation into species abundance-relationships, food web descriptions, and existing knowledge of the field site suggest a stable system (Chapters 2,3,4). Consequently in contrast to Makarieva *et al.* (2004) it is likely high *b* values for the slope of density-body size regressions are not typical of highly disturbed environments. To the contrary, they may be evidence of stable systems. This suggests 'energy equivalence' may not be a stable state for communities and crucially metabolic constraints are not important in shaping the structure and dynamics of real systems. Rather, the complex interplay between diversity, stability and productivity, may determine the distribution and dynamics of energy within systems, while, energy may in turn influence these three ecosystem properties.

Table 11. Kernel body size-density distribution estimates of macrophyte stand sample replicates taken from April 2004 through March 2005 in the River Lambourn. (h = kernel function critical band, m = least number of modes for which the bootstrap test was not significant at a 5% level, P = level of significance for each mode number)

Month	n	Modes	Hc	P	Month	n	Modes	Hc	P
April 2004	1	1	1.49	0.34	December 2004	1	2	0.63	0.73
	2	2	0.97	0.35		2	2	0.78	0.52
	3	3	0.60	0.19		3	2	0.41	0.69
	4	2	0.88	0.27		4	1	1.82	0.21
May 2004	1	2	0.90	0.18		5	2	0.50	0.57
	2	1	1.72	0.16		6	3	0.14	0.58
	3	2	0.76	0.53		7	2	0.63	0.66
	4	2	0.62	0.37	January 2005	1	2	0.49	0.70
	5	2	0.90	0.25		2	1	1.85	0.21
	6	2	0.68	0.69		3	2	0.73	0.53
	7	2	0.83	0.52		4	2	0.71	0.44
June 2004	8	2	0.73	0.41		5	1	1.78	0.12
	9	2	0.27	0.98		6	2	0.96	0.31
	10	2	0.56	0.69	February 2005	1	3	0.77	0.09
July 2004	1	2	0.66	0.42		2	2	0.87	0.37
	2	2	1.12	0.14		3	2	0.60	0.65
	3	2	0.73	0.50		4	2	0.59	0.53
August 2004	1	2	0.35	0.89		5	2	0.76	0.50
	2	2	1.33	0.14		6	2	0.63	0.64
	3	2	0.78	0.35		7	2	0.93	0.35
	4	2	0.91	0.37		8	2	0.68	0.72
	5	2	0.73	0.53	March 2005	1	2	0.88	0.31
September 2004	1	2	1.14	0.43		2	3	0.51	0.61
	2	2	1.03	0.08		3	1	1.39	0.52
	3	2	0.96	0.38		4	2	0.67	0.68
	4	2	0.33	0.88		5	2	0.94	0.32
	5	2	0.60	0.66		6	3	0.53	0.54
	6	2	0.89	0.20		7	1	1.46	0.30
	7	2	0.51	0.55					
	8	2	0.90	0.36					
October 2004	1	2	0.88	0.43					
	2	2	1.05	0.19					
	3	2	0.64	0.71					
	4	2	0.55	0.45					
	5	2	1.04	0.16					
	6	2	1.01	0.20					
	7	1	1.72	0.28					
November 2004	1	2	1.10	0.15					
	2	2	0.88	0.32					
	3	2	0.80	0.30					
	4	2	0.84	0.45					
	5	2	1.24	0.10					
	6	2	0.67	0.32					

Table 12. Kernel body size-density distribution estimates of gravel bed sample replicates taken from April 2004 through March 2005 in the River Lambourn. (h = kernel function critical band, m = least number of modes for which the bootstrap test was not significant at a 5% level, P = level of significance for each mode number)

Month	n	Modes	Hc	P	Month	n	Modes	Hc	P
April 2004	1	2	0.9	0.40	December 2004	1	2	0.7	0.51
	2	1	1.6	0.22		2	2	0.6	0.66
	3	2	0.9	0.42		3	2	0.8	0.61
	4	2	0.4	0.36		4	2	0.8	0.37
	5	1	1.5	0.34		5	2	0.8	0.61
May 2004	1	2	0.5	0.93	January 2005	1	2	0.7	0.86
	2	2	0.7	0.53		2	3	0.4	0.76
	3	2	0.7	0.42		3	2	0.8	0.64
	4	2	0.4	0.91		4	2	1.3	0.26
	5	2	0.6	0.66		5	3	0.4	0.31
June 2004	1	2	0.8	0.57	February 2005	1	2	1.06	0.26
	2	3	0.5	0.68		2	2	0.95	0.47
	3	3	0.5	0.29		3	2	0.78	0.47
	4	3	0.3	0.87		4	1	1.95	0.18
July 2004	1	2	0.7	0.76	March 2005	1	2	0.59	0.75
	2	2	0.6	0.61		2	2	0.87	0.47
	3	2	0.6	0.39		3	2	0.91	0.48
	4	2	0.7	0.40		4	2	0.72	0.35
	5	2	0.6	0.77		5	2	0.53	0.52
	6	2	1	0.32					
	7	3	0.6	0.35					
	8	2	0.9	0.39					
August 2004	1	2	0.9	0.48					
	2	2	0.6	0.53					
	3	3	0.4	0.30					
	4	2	1.2	0.16					
	5	2	0.9	0.63					
	6	2	0.8	0.52					
	7	2	0.8	0.54					
September 2004	1	2	1.1	0.24					
	2	2	0.6	0.62					
	3	2	0.7	0.63					
October 2004	1	3	0.4	0.46					
	2	2	1.2	0.17					
	3	2	0.7	0.69					
	4	2	0.8	0.49					
	5	2	0.9	0.38					
November 2004	1	2	0.7	0.53					
	2	2	0.8	0.27					
	3	2	1	0.36					
	4	2	0.8	0.53					
	5	2	0.5	0.50					
	6	2	0.8	0.63					

Table 13. OLS regression slopes and intercepts for the seasonal and annual relationship between $\log_{10}$ mean body size (μg dry mass) and $\log_{10}$ mean species density (ind. m^{-2}) for benthic invertebrate assemblages within macrophyte stands and gravel beds of the river Lambourn. (*n*, number of species; r^2 proportion of variance explained by the correlation of density with body size; *b*, OLS regression slope; *b* ± *95% C.L.*, 95% confidence limits for prediction of the mean slope; *a*, OLS intercept; *a* ± *95% C.L.*, 95% confidence limits for prediction of the intercept; all regression slopes were statistically significant at $P < 0.01$ and significantly different from the -2/3, -3/4 and -1 exponents, *t*-test $P > 0.05$)

	Macrophyte						Gravel					
Season	*n*	r^2	*b*	*b* ± *95% C.L.*	*a*	± *95% C.L.*	*n*	r^2	*b*	± *95% C.L.*	*a*	*a* ± *95% C.L.*
Spring	72	0.543	-0.371	0.081	2.820	0.182	69	0.620	-0.394	0.072	2.882	0.151
Summer	86	0.592	-0.377	0.068	2.927	0.152	48	0.572	-0.355	0.091	2.880	0.172
Autumn	67	0.600	-0.417	0.072	3.022	0.177	43	0.524	-0.357	0.107	2.930	0.200
Winter	46	0.681	-0.450	0.093	3.132	0.193	56	0.669	-0.411	0.078	2.870	0.152
Annual	125	0.644	-0.396	0.052	2.935	0.116	96	0.470	-0.348	0.068	2.864	0.127

Table 14. RMA regression slopes for the seasonal and annual relationship between $\log_{10}$ mean body size (µg dry mass) and $\log_{10}$ mean species density (ind. m^{-2}) for benthic invertebrate assemblages within macrophyte stands and gravel beds of the river Lambourn. (*n*, number of species; r^2 proportion of variance explained by the correlation of density with body size; *b*, RMA regression slope; *b* ± *95% C.L.*, 95% confidence limits for prediction of the mean slope; regression slopes were all statistically significant at $P < 0.01$ and significantly different from the RMA -1 exponent of energy equivalence, *t*-test $P > 0.05$)

	Macrophyte				Gravel			
	n	r^2	*b*	*b* ± *95% C.L.*	*n*	r^2	*b*	*b* ± *95% C.L.*
Spring	72	0.543	-0.503	0.083	69	0.640	-0.493	0.073
Summer	86	0.592	-0.490	0.070	48	0.572	-0.469	0.091
Autumn	67	0.601	-0.538	0.098	43	0.524	-0.493	0.107
Winter	46	0.682	-0.545	0.108	56	0.669	-0.503	0.079
Annual	125	0.644	-0.493	0.054	96	0.520	-0.483	0.068

Table 15. MANCOVA results of comparisons between macrophyte stands and gravel beds in the River Lambourn seasonally for density-body size distributions and standing biomass-body size relationships. (*df*, degrees of freedom; *F*, *F* test of the relationship of density with body size; *P*, significance of *F* test = *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$)

Macrophyte vs Gravel Comparisons	*df*	*F*	*P*
Seasonally			
Habitat	1,478	0.117	0.733
Season	3,478	2.327	0.074
Season*Habitat	3,478	0.193	0.901

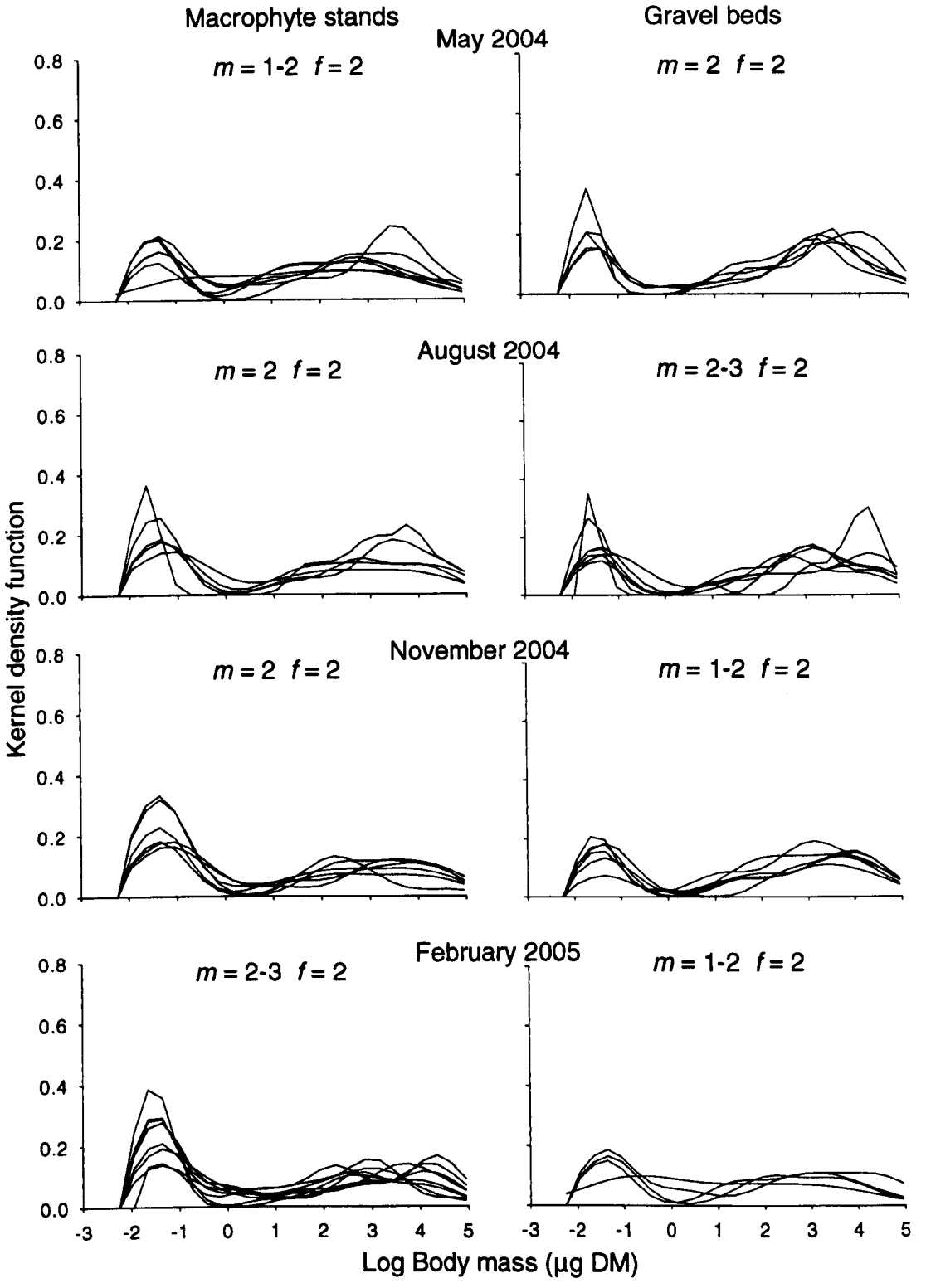

Figure 25. Kernel density functions fitted to density-body size distributions of individual samples from four months for macrophyte stands and gravel beds in the river Lambourn. The range of different modes found, *m*, are shown along with the most frequent mode found in each habitat each month, *f*. See Table 2 for statistical details of all months.

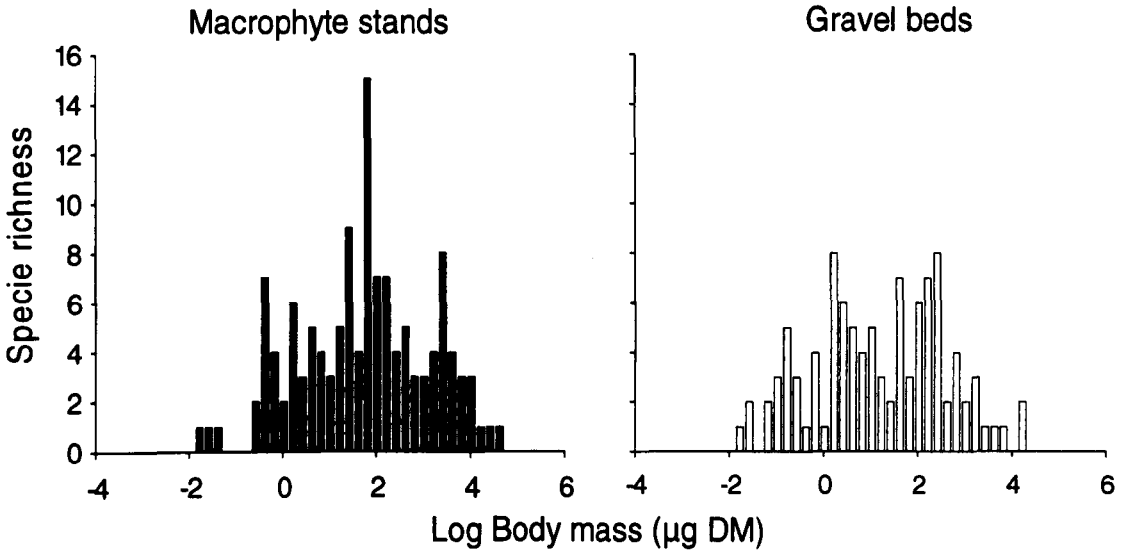

Figure 26. Annual relationship of species richness with body size distribution from pooled monthly data for macrophyte stands (black bars) and gravel beds (white bars).

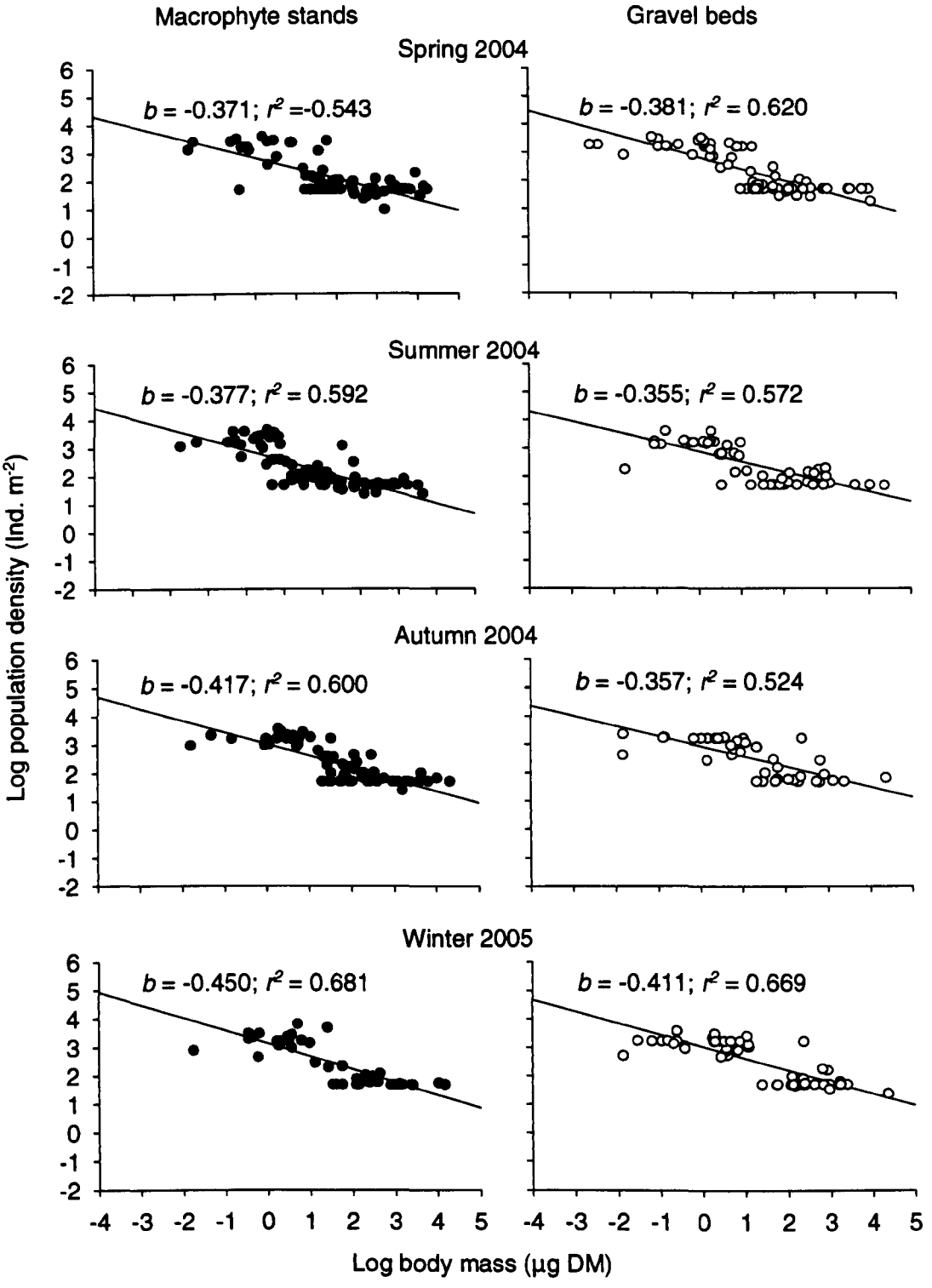

Figure 27. Seasonal linear regressions of $\log_{10}$ population density against $\log_{10}$ body mass of benthic invertebrates from macrophyte stands (black circles) and gravel beds (white circles) from within the River Lambourn. OLS regression lines are displayed, all regressions were statistically significant ($P < 0.05$).

CHAPTER 6: PRODUCTION/BIOMASS ALLOMETRY OF A WHOLE METAZOAN CHALK STREAM INVERTEBRATE COMMUNITY

ABSTRACT

Very little synthesis of body size allometry and production has occurred despite a commonality of focus on energetics. In this chapter, production, standing biomass, and annual P/B body size allometry of benthic invertebrates within a chalk stream are investigated. For the first time, the analysis of allometric relationships is extended over a large spectrum of body size from meiofauna to macrofauna within a freshwater system. The aim was to test *a priori* hypotheses predicted by metabolic theory concerning the shape of the allometric relationships. P/B allometry closely conformed to metabolic predictions over the whole spectrum of body size. A divergent pattern was found between the size classes however, with P/B exponents for macrofauna more positive than theoretical predictions and meiofauna more negative. Paradoxically neither production or standing biomass fitted the predictions of metabolic theory. Combined with the results of a previous publication from the same system, the data indicate the interrelationships of diversity, stability, and trophic structure, is more important in determining density-body size distributions than metabolic constraints.

INTRODUCTION

Numerous investigations of energy flow measured as production of tissue or biomass elaborated per unit time have been conducted since the seminal paper of Lindeman (1942) on the trophic basis of production in ecosystems. Meanwhile, considerable scientific effort as been devoted to proving or disproving aspects of body size allometry (see Brown *et al.* 2004), in particular density-body size relationships which led Damuth (1981) to describe the 'energy equivalence rule'. The energy equivalence rule states "all species within a community use the same amount of energy irrespective of average body size". Despite the obvious commonality between production and density-body size investigations, i.e. the focus on energy flow, little synthesis in the approaches used by Lindeman (1942) and Damuth (1981) to studying natural systems has taken place with notable exceptions (Banse and Mosher, 1980; Humphreys, 1981; Dickie *et al.* 1987; Plante and Downing, 1989; Morin and Bourassa, 1992; Benke, 1993).

Dickie (1972) first suggested scaling the ratio of production divided by biomass (P/B), otherwise known as the tissue turnover rate with body size in marine fish. Some influence of life-length or age at maturity on the P/B-body size exponent and one regression line fitting all taxa irrespective of body size was predicted (Dickie, 1972). Work on comparative physiology and scaling of maximum population growth rate, r_{max}, which is equivalent to P/B, yielded a theoretical exponent of -0.25 (Fenchel, 1974; Brown *et al.* 2004). However in the first attempt at scaling log P/B across a wide range of body size and diverse phylogenetic groups, Banse and Mosher (1980) rejected these findings in favour of an exponent of -0.37. This implies that smaller species perform better (i.e. have faster biomass turnover rates) than larger ones.

Schwinghamer *et al.* (1986) extended the P/B body size analysis from intertidal macroinvertebrates down to meiofauna and bacteria and found a negative P/B-body size

relationship of -0.30 using coarse taxonomic groups. This was not significantly different from the exponent of Banse and Mosher (1980). Furthermore they reported an all taxa regression with an exponent of -0.17. Revisiting the analysis of Banse and Mosher (1980) with additional fish data from Humphreys (1979) and meiofauna data from Schwinghamer *et al.* (1986) an all taxa regression exponent of -0.18 was found by Dickie *et al.* (1987). This was not significantly different from the theoretically predicted value of -0.25 which led them to conclude the all taxa P/B regression line represented an important general physiological scaling for invertebrates groups.

However, Peters (1983) demonstrated earlier that changing taxonomic resolution, as well as the inclusion and exclusion of exotic taxa, significantly changes the exponent of P/B-body size relationships. While all the analyses described so far had a low number of observations (<100 species) contrasting with Cusson and Bourget (2005) who using 352 observations for marine taxa globally found a P/B-body size exponent of 0.08. Meanwhile three freshwater studies with significantly higher numbers of observations have produced confusing results. An exponent of -0.16 for lentic invertebrates was found with 164 observations (Plante and Downing, 1989). While for lotic invertebrates a value of -0.34 was estimated with 291 observations of average individual biomass (Morin and Bourassa, 1992), and another value of -0.247 using 1,565 observations of maximum individual weight (Benke, 1993).

Freshwater analyses have also found a positive association between production, mean or maximum body size and temperature (Plante and Downing, 1987; Morin and Bourassa, 1992; Benke, 1993). More recently, development of metabolic theory has predicted an exponent of 0.75 for the production-body size relationship (Brown *et al.* 2004). This is because a constant fraction of an organism's metabolism is devoted to production, and the metabolic theory predicts that individuals of equal body size have

roughly equal metabolic rates. Moreover, Ernest *et al.* (2003) have analysed a data set of temperature-corrected production values for a wide range of taxa from unicells to mammals spanning many terrestrial and aquatic habitats and found an exponent of 0.757.

Originally, the metabolic theory also predicted that standing stock or stored biomass scaled with body size yielding an exponent of -0.25 (Brown *et al.* 2004). However, work within many marine pelagic systems showed total standing biomass to be invariant in relation to body size (Sheldon *et al.* 1972; Cyr, 2000). Subsequently this discrepancy was explained by the integration of a correction factor for the loss of energy between trophic levels due to inefficient transfer known as the "Lindeman efficiency". Within trophic levels density allometry is predicted to yield an exponent of -0.75, and biomass -0.25, whereas across trophic levels density scales as -1 and biomass is now predicted to be invariant (Brown *et al.* 2004).

However, standing biomass scales positively with production and has been demonstrated as a better predictor than temperature or even individual body size (Plante and Downing, 1989; Morin and Bourassa, 1992; Benke, 1993; Cusson and Bourget, 2005). Plante and Downing (1989) were able to predict 63% of the variance in log P with standing biomass while Morin and Bourassa (1992) predicted 79%. Benke (1993) was able to predict 86% of production variance with standing biomass, with temperature and maximum individual weight predicting less than 10%. While Cusson and Bourget (2005) found 75% of the variance in body size was explained by biomass.

Currently no freshwater studies have been carried out with a body size spectrum extending over meiofaunal size to test the relationships outlined above. Recent investigations have revealed much higher freshwater macroinvertebrate P/B estimates than previously expected (Huryn and Wallace, 2000). P/B values of 157 to 258 for riverine chironomids and 208 to 347 for lotic benthic rotifers have been found (Benke, 1993;

Chapter, 3). Values for many freshwater meiofauna species significantly greater than previous conservative estimates of 9 or 10 (McIntyre, 1964; Gerlach, 1971; Waters, 1977, Banse and Mosher, 1980) are being documented (Stead *et al.* 2005; Reiss, 2006). Consequently, the inclusion of meiofauna could considerably alter relationships predicted by previous work and need testing.

Moreover, by their very nature the meta-analyses of P/B-body size relationships conducted so far have relied upon disparate sources of data. This adds a number of extra potential levels of error to analyses. Data from different information sources may have been obtained using different sampling techniques and production estimation methods. Moreover, Banse and Mosher (1980) as well as Dickie *et al.* (1987) recognised the importance of spatial and distributional variation. While environmental factors such as temperature may be corrected for, it is much harder to quantify and correct for the effects on communities of varying food availability, nutritional quality, and the impacts of fluctuating predation pressure.

In this chapter findings are presented of an investigation into the body size scaling relationships of annual P/B, production, and standing biomass of benthic invertebrates from two stream habitats, macrophyte stands and gravel beds. The data were all obtained over a one year period from the same study site, a chalk stream in southern England. Moreover, a standard sampling technique and production estimation method was used. Consequently we can be confident the analysis has minimised error associated with meta-analyses such as varied sampling techniques and environmental conditions between studies. Moreover, the data set is highly resolved to species wherever possible for both meiofauna and macrofauna, totalling 120 observations for macrophyte stands and 96 for gravel beds. We can therefore rigorously test for the first time in a freshwater lotic environment whether the

theoretical exponents for production (3/4), standing biomass (0, 1/4) and P/B (-1/4) hold over a body size spectrum including both macrofauna and meiofauna.

MATERIALS AND METHODS

Study area

The study area was an 80 m reach of the groundwater fed, cretaceous chalk stream River Lambourn as it passes through Bagnor ($51^0$25'29"N, $1^0$21'08"E) near Newbury in Southern England. The catchment is dominated by agricultural practices and is hypernutrified (Pretty *et al.* 2006) with a circumneutral pH (Chapter 2). The range of water temperature over the study period was between 7 and 15^0C, a maximum depth of 0.4 m was recorded, and channel width varied 3 to 6 m. Riparian vegetation either side of the stream consisted of a wetland and Salix *spp.* dominated woodland. Discharge was stable and there was no well defined riffle-pool sequence, main bed heterogeneity being caused by growth of lotic macrophyte stands of *Ranunculus* sp., *Berula erecta* (Hudson) Coville, and *Callitriche spp.*

Sampling

Quantitative benthic samples of the whole metazoan community (>42 μm) were taken every month from April 2004 to March 2005 with a modified Hess sampler (surface area: 2.71 dm^2; mesh size 42 μm). This device is effective to a 5 cm depth into the streambed and was used to sample both gravel beds and macrophyte stands. The sampling design formed part of a larger study into surface-subsurface exchange in rivers (Pretty *et al.* 2006; Chapter 2). Consequently although macrophyte growth was unpredictable over the study period a fixed sampling design was used. This involved twelve 2 m x 6 m sampling areas spaced at 7 m intervals along a longitudinal gradient of the stream channel. One Hess sample was taken at random within each sampling area with habitat type recorded. In total 76 gravel

bed samples and 62 macrophyte stand samples were taken as complications with sampling apparatus were encountered in June (7 samples) and July (11 samples).

Samples were all kept cool during transport to the lab where they were immediately sieved into meiofaunal fractions (>42 um <500 μm) and macrofaunal fractions (>500 μm). Meiofauna fractions were refrigerated and sorted live to enable enumeration of soft-bodied taxa which are lost when fixatives and preservatives are added. The macrofauna fractions were immediately preserved in ethanol for processing after the meiofauna. During enumeration and identification, both meiofauna and macrofauna individuals were measured to the nearest micrometer using either an Olympus BX50 (Olympus Optical, Tokyo, Japan) (1250x magnification) microscope, or a dissecting microscope (25-250x magnification). However soft-bodied meiofauna had to be measured to the nearest micrometer using the Olympus BX50 and identified where possible to species from video recordings. These were recorded with 3CCD JVC video camera (JVC, Tokyo, Japan), which was connected to the microscope. Chironomidae and Oligochaeta were measured using a dissecting microscope, but had to be fixed on slides in Euparal for identification. Finally some highly abundant taxa (>30 individuals found across all samples from a substrate type in one month) were randomly subsampled and measured to obtain a population size frequency distribution approximating a 10% sampling error of the mean (Elliot, 1977). Measurements were converted to dry mass using published regressions and conversions presented in Chapter 3 where detailed descriptions of the sampling design, sample processing and taxonomic designations can also be found.

Production calculations

Many of the taxa in the River Lambourn displayed no discrete cohorts throughout the year (S.Tod. pers. obs.), so the size frequency method of Hynes and Coleman (1968) which

assumes average cohorts was used to estimate production. The method was applied to all taxa irrespective of whether discrete cohorts were identifiable to maintain consistency. Based on individual body mass, taxonomic groups were divided into ten equal size classes for which annual mean density and biomass values were estimated as instructed in the method of Hynes and Coleman (1968) with the modifications of Hamilton (1969). From these frequency tables annual production and standing biomass were then estimated. Following Hamilton (1969) and Benke (1979) production estimates were made at the lowest practicable taxonomic level to reduce error associated with lumping species variable in maximum attainable body size and generation times.

Minimum and maximum production estimates were made using Cohort Production Intervals (CPI's) which correct for deviations in generation time, and/or periods of lifespan not contributing to benthic production over a 365 day period (Benke, 1979). Published life-history data for taxa which most closely matched those found in the River Lambourn, and for which a similar thermal regime was found were used. CPI's, minimum and maximum generation times, production estimates, and standing biomass values can be found Chapter 3.

Statistical Analyses and Construction of Size Distributions

All population density data were converted to individuals per metre squared to standardise units used in estimates of production and biomass. Body size was converted from dry mass to kilocalories assuming 1 g live mass is equal to 1.5 Kcal (Banse and Mosher, 1980), and wet mass is equal to live mass with a dry mass to wet mass conversion of 0.25 (Reiss, 2006). Both body size axes were used to facilitate comparison with publications which used only one of the two different body scaling units. P/B, production, standing biomass, and Kcal equivalent body size were log transformed and then ordinary least squares regressions

(OLS) were performed using Statistica (Statsoft Inc. USA). *t*-tests were used to examine goodness of fit to the theoretical scaling exponents for production, standing biomass, and P/B.

RESULTS

P/B allometry

The minimum and maximum P/B-body size regressions for the whole invertebrate communities of the macrophyte stands and gravel beds were highly significant (Table 16, Fig. 28a; $P = <0.001$). All of the whole invertebrate community P/B analyses yielded scaling exponents not significantly different from the theoretical prediction of -1/4 (Table 16, Fig. 28a; $P > 0.05$), except the macrophyte stand minimum estimate of -0.152 (*t*-test, $P < 0.05$) (Table 16, Fig. 28a).

When examining by invertebrate size classes, the gravel bed meiofauna and macrofauna regressions using the minimum P/B estimate were significantly different from -1/4 (*t*-test, $P < 0.05$) (Table 16). The macrophyte stand meiofauna minimum P/B estimate and gravel bed macrofauna maximum P/B estimate did not produce significant regressions (Table 16; $P > 0.05$). The r^2 values for all regressions were fairly low but generally improved when taxa were pooled ranging between 0.281 and 0.484 (Table 16, Fig. 28a). Meiofauna slopes were significantly steeper than those of macrofauna in both habitats, and with both minimum and maximum P/B estimates (Table 16).

Production and standing biomass both scaled positively with body size (Table 17, Fig. 28b,c). None of the production estimates scaled consistently with the 3/4 value of metabolic theory (*t*-test, $P < 0.05$) (Table 17, Fig. 28b). The r^2 values ranging 0.211 to 0.585 suggested a fairly weak relationship between production and body size (Table 17, Fig. 28b).

Log standing biomass estimates generally correlated better with body size than the production estimates within both habitats, with r^2 values of 0.422 and 0.557 for the macrophyte stands and gravel beds respectively (Table 17, Fig. 28c). However, the positive annual standing biomass-body size exponents of 0.635 in the macrophyte stands and 0.717 in the gravel beds indicated no conformance to the 0.25 exponents of the theoretical scaling relationship (*t*-tests, $P < 0.05$) (Table 17, Fig. 28c). As in previous investigations of freshwater environments, standing biomass was found to be the best descriptor of annual production, r^2 values ranging 0.832 to 0.907 with positive exponents of between 0.752 and 0.862 (Table 17, Fig. 29).

DISCUSSION

Close to -1/4 scaling of P/B with body size for the whole invertebrate community of both macrophyte stands and gravel beds in the River Lambourn was found. A pattern of more negative slopes for the meiofauna than macrofauna P/B-body size relationship was also documented. Furthermore, production and standing biomass were both positively correlated with body size but indicated no conformance to theoretical predictions of metabolic theory. Production was much more strongly correlated with standing biomass than body size.

P/B allometry

Various authors have analysed the relationship between r_{max} and body size finding close agreement with the theoretical exponent of -0.25 (see Peters, 1983). Banse and Mosher (1980) rejected these findings in favour of an exponent of -0.37 based on their P/B analysis, implying that smaller species perform better (i.e. have faster biomass turnover rates) than larger ones. Both Fenchel (1974), and Banse and Mosher (1980) found significant differences in elevation of slopes for specific groups of taxa (e.g. fish and mammals). This

led Banse and Mosher (1980) to predict an ecological explanation for the P/B-body size relationship where smaller species have differing birth schedules, environmentally regulated growth rates, and size-dependent, predation-controlled mortality.

However, Schwinghamer *et al.* (1986) and Dickie *et al.* (1987) recognised the significance of an all taxa regression of P/B with body size which the latter concluded represents an important general physiological scaling for invertebrates groups. All taxa regressions of P/B with body size yielded similar exponents for Schwinghamer *et al.* (1986) and Dickie *et al.* (1987) of -0.17 and -0.18 respectively, not significantly different from -1/4. However, more recent analyses with larger numbers of observations have yielded mixed results, exponents ranging between -0.34 and 0.08 (Morin and Bourassa, 1992; Cusson and Bourget, 2005).

This study is the first not to rely upon disparate sources of information to derive data for analysis, thereby minimising the confounding effects of spatial and temporal variation in environmental and ecological factors on P/B estimates for species. A good agreement between whole community regressions of P/B with body size and the theoretical scaling exponent of -1/4 was found (Fenchel, 1974; Brown *et al.* 2004). This suggests that the high meiofauna P/B estimates made in Chapter 3 and for other lotic invertebrate taxa by various researchers are probably reasonably accurate (Benke, 1993; Stead *et al.* 2005; Reiss, 2006).

Both Schwinghamer *et al.* (1986) and Dickie *et al.* (1987) found that within taxonomic groups the exponents were significantly more negative than the all taxa regression line. Dickie *et al.* (1987) hypothesised the variation between groups was due to additional ecological scaling factors associated with spatial variation or distribution of organisms and their food resources. Within the River Lambourn a different pattern was found where exponents for meiofauna P/B-body size relationships were significantly more

negative than those of the whole community regressions, while macrofauna exponents were more positive. This suggests previous investigations of freshwater invertebrate communities may have significantly overestimated the exponent for the P/B-body size relationship, a steeper more negative slope for previous analyses possibly being expected.

Furthermore, the findings suggest tissue turnover rates increased faster per unit log mass decrease in the meiofaunal size class than the macrofaunal size class. This could be due to different ecological scaling factors as proposed by Dickie *et al.* (1997). Stead *et al.* (2005) found evidence for this in an acid stream where meiofauna and macrofauna responded differently to fluctuating environmental variables resulting in highly unstable density-size spectra.

However, previous investigations showed synchronous seasonal fluctuations in density of meiofauna and macrofauna, as well as stable bimodal density-size spectra in the River Lambourn (Chapters 2,3). Furthermore, in Chapter 5 the -3/4 and -1 scaling values of metabolic theory for the invertebrate communities of macrophyte stands and gravel beds in the River Lambourn were rejected. Exponents ranged between -0.450 and -0.348, in addition production and standing biomass were shown to be dominated by macroinvertebrates within this chalk stream (Chapter 3). It is therefore possible that the density-body size relationships were driven by relatively much lower densities of meiofauna than macrofauna, possibly as a result of predation by larger taxa. In turn, reduced population pressure may have resulted in the relatively much higher tissue turnover rates for meiofauna when compared to macrofauna. However, few studies of density dependence in meiofauna populations have been conducted with much uncertainty remaining (Silver *et al.* 2002).

Production and standing biomass

Temperature-corrected production has been shown to scale closely with the theoretical exponent of 3/4 for a wide range of taxa from fish, birds, mammals, zooplankton and plants (Ernest *et al.* 2003). Within the River Lambourn the production values were not temperature corrected, however, none of the production estimates were close to the 3/4 predicted value of metabolic theory. Moreover, standing biomass estimates were highly significantly correlated positively with body size rejecting both the invariant and 1/4 scaling values.

The production and standing biomass results are consistent with the rejection of metabolic theory for explaining density-body size allometry in the River Lambourn (Chapter 5). Furthermore, the combination of exponents for standing biomass and density should balance out equalling 1. Good agreement for the macrophyte stands with a value of 1.031 and gravel beds with a value of 1.065 was found.

In Chapter 5 it was suggested the most likely explanation for the imbalance in distribution of energy between body sizes in the River Lambourn may be the result of a combination of interrelated factors. From Chapters 2,3,4, and 5, the invertebrate assemblage of the River Lambourn was found to be stable, highly diverse and consequently complex, with a high level of connectance in food webs, and a predominantly generalist feeding strategy. Furthermore, in Chapter 5 it was postulated that this resulted in a high number of weak, and few strong, interactions in terms of trophic relationships. The logical result would be an unequal share of energy between taxa which were supported by investigations of density, biomass and production, all dominated by a few taxonomic groups within the community.

The generalist feeding and dominance of a few species suggested high functional redundancy. The food webs of Chapter 4 contained more intermediate and basal species

than top, suggesting any functional redundancy was biased towards lower trophic levels. Furthermore, a positive relationship between body size and increasing trophic position within communities has been established for a variety of systems (Warren and Lawton, 2004; Woodward *et al.* 2005; Jennings *et al.* 2007), therefore greater functional redundancy should be found in smaller body size classes. A bias in distribution of strong and weak 'interactors' can also be predicted due to a combination of fractal geometry influencing the resource base of species differently relative to their body size, and 'Lindeman efficiency' limiting energy availability to higher trophic levels. Consequently shallow density-body size exponents and steeper more positive biomass exponents like those found in the River Lambourn may be expected for stable communities. In terms of production, the lack of functional redundancy and species richness in the higher trophic levels, combined with slower tissue turnover rates because of the larger size of these taxa, may contribute towards shallower production-body size exponents than predicted by metabolic theory.

Utility of predictive models

Benke (1993) argues that as production is likely to be function of biomass then the explanation of most of the variance in the former by the latter should be expected. Various authors reviewed in Benke (1993) have suggested that the relationships between standing biomass, P/B and body size may be used as quick non-labour intensive method to predict production for communities. Good correlations between production and standing biomass have been found by Plante and Downing (1989), Morin and Bourassa, (1992), Benke (1993), and Cusson and Bourget (2005). Similarly, in this study standing biomass explained a significant amount of the variance in production estimates of between 0.831 and 0.907.

Various researchers have advocated or used correlative relationships between body size, standing biomass, and P/B, to estimate production (Peters, 1983; Plante and Downing,

1989; Morin and Nadon, 1991; Morin and Bourassa, 1992; Rasmussen, 1993). The main advantage being quick and easy estimation of production which is usually time consuming, labour intensive, and can be expensive. Benke (1993) strongly argued against such an approach for estimating production and calculated taxon specific production and model predictions calculating an error of greater than 300% with the latter method.

Since Benke (1993) some attempts at refining and applying predictive models to estimates of production for various groups have occurred (Zimmer *et al.* 2001; Randall, 2002). However, I would still strongly argue in favour of the conclusion of Benke (1993). Banse and Mosher (1980) clearly stated the exponents for P/B-body size allometry had not been rigorously tested. This still remains true today as the findings presented here evidence in revealing a different pattern from previous analyses where meiofauna exponents differ from the whole community, and the macrofauna. Yet more analyses of larger datasets including meiofauna from a wider array of systems and smaller microfauna may alter the value of exponents even further. Significant advances need to be made in synthesising the production estimation and body size allometry approaches of investigating communities before reliable predictions can be made from one to other.

Concluding remarks

A good agreement with metabolic theory for P/B scaling but not standing biomass and production was found. In Chapter 5, no fit to metabolic theory for density-body size relationships was found. Moreover, as described earlier, there seems to be a logical link between the rejection of metabolic theory for the density, biomass and production allometric relationships and our existing knowledge relating to the form and function of the benthic invertebrate assemblages. However, at the level of the individual there must be physiological limits of body size and metabolism. For example, the rate of growth of an

individual cannot increase *ad infinitum* with greater resource availability. This is because limitations of biological adaptations for assimilation and foraging may limit growth. These limits may well be reflected in the fit of the overall P/B-body size relationships to the predictions of metabolic theory. However, the data suggest other factors can play more important roles in determining the structure and function of biological systems at the community or ecosystem level. In particular, the potential correlation between stability and the form of allometric relationships within communities needs addressing, as it may provide useful insights into better conservation management practices in an increasingly uncertain world.

Table 16. Regression summaries for analyses of minimum and maximum annual P/B estimates against body size for the whole invertebrate community inhabiting macrophyte stands and gravels beds, as well as meiofauna and macrofauna separately, for the River Lambourn. (n, number of species; r^2, coefficient of determination; b, OLS regression slope; plus 95% confidence limits; t-test, $P < 0.05$ for b values significantly different from -0.25 are indicated by X)

P/B-Body size regressions	n	r^2	b	± 95% C.L.	df	F	P
Macrophyte stands							
P/B Minimum							
All taxa	120	0.281	-0.152 X	0.089	1,120	46.144	<0.001
Meiofauna	36	0.183	-0.292	0.430	1,34	7.595	0.316
Macrofauna	84	0.132	-0.127	0.144	1,82	12.451	<0.001
P/B Maximum							
All taxa	120	0.460	-0.238	0.094	1,120	100.72	<0.001
Meiofauna	36	0.216	-0.326	0.432	1,34	9.378	<0.01
Macrofauna	84	0.207	-0.183	0.158	1,82	21.354	<0.001
Gravel beds							
P/B Minimum							
All taxa	96	0.379	-0.197	0.103	1,96	52.971	<0.001
Meiofauna	46	0.439	-0.393 X	0.270	1,44	34.491	<0.001
Macrofauna	50	0.083	-0.113 X	0.218	1,48	4.379	<0.05
P/B Max							
All taxa	96	0.484	-0.257	0.108	1,96	85.701	<0.001
Meiofauna	46	0.283	-0.306	0.296	1,44	17.410	<0.001
Macrofauna	50	0.135	-0.171	0.251	1,48	7.540	0.177

Table 17. Regression summaries for analyses of annual mean minimum and maximum production estimates and standing biomass against body size, and production estimates against standing biomass for the macrophyte stand and gravel beds whole communities within the River Lambourn. (n, number of species; r^2 correlation of variable with body size; b, OLS regression slope; plus 95% confidence limits) (All annual production exponents significantly departed from 0.75 and all standing biomass exponents from 0.25; t-test, $P < 0.05$).

Body size regressions	n	r^2	b	± 95% C.L.
Macrophyte stands				
Production Min	120	0.301	0.486	0.135
Production Max	120	0.211	0.390	0.137
Standing biomass	120	0.422	0.635	0.135
Gravel beds				
Production Min	96	0.390	0.513	0.131
Production Max	96	0.585	0.463	0.131
Standing biomass	96	0.557	0.717	0.131
Standing biomass regressions				
Macrophyte stands				
Production Min	120	0.907	0.862	0.050
Production Max	120	0.865	0.807	0.058
Gravel beds				
Production Min	96	0.855	0.791	0.066
Production Max	96	0.832	0.752	0.069

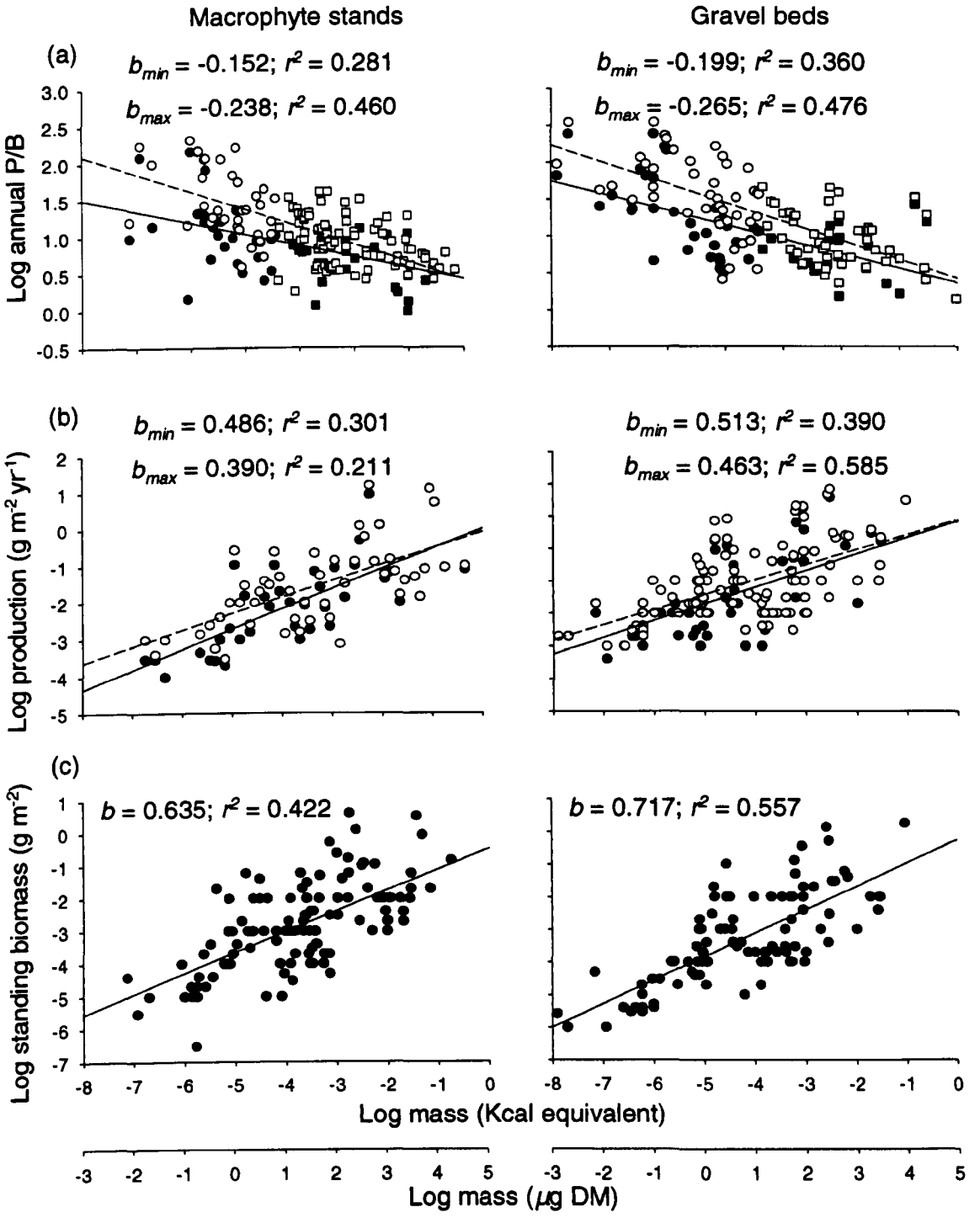

Figure 28. Body size allometry for annual log P/B (a), log production (b), and log standing biomass (c), for macrophyte stands and gravel beds in the River Lambourn. For (a) and (b) closed symbols equal minimum estimates and open symbols maximum estimates, whilst squares denote macrofauna and circles meiofauna for (a). (r^2 and b values are displayed with minimum / maximum estimates and regressions, broken lines indicating regressions of maximum values where applicable)

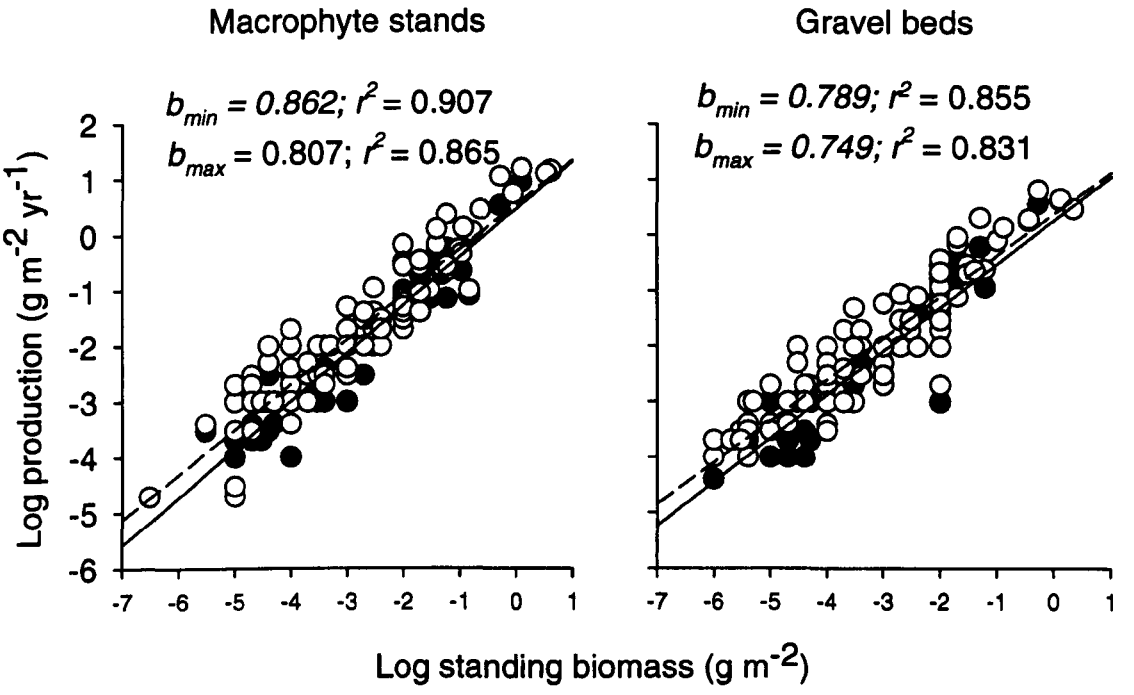

Figure 29. Relationships of minimum (filled circles/solid line) and maximum (open circles/dotted line) production estimates against annual standing biomass for macrophyte stands and gravel beds in the River Lambourn. (r^2 and *b* values are displayed with minimum / maximum estimates and regressions, broken lines indicating regressions of maximum estimates)

CHAPTER 7: GENERAL DISCUSSION

Recent investigations have highlighted the importance of meiofauna and the varied roles they play in communities and ecosystems (Dole-Olivier *et al.* 1997; Hakenkamp and Palmer 2000; Schmid-Araya *et al.* 2002a; Stead *et al.* 2005a; Stead *et al.* 2005b). In this study the primary aim was to provide the first detailed account of lotic meiofauna in chalk streams with an assessment of their importance relative to that of the macrofauna, and with regards to ecosystem function.

The hyporheic zone

In the only other chalk stream study focussing on hyporheic invertebrates, Bird (1982) found a limited depth distribution and low densities of the oligochaete *Propappus volki* Michaelsen. Similarly, from Chapter 2 very low densities of macroinvertebrates within the hyporheic zone of the River Lambourn were found and meiofaunal abundances decreased rapidly with depth from 10 cm. Furthermore, Pretty *et al.* (2006) reported low biogeochemical activity within the hyporheic zone of the River Lambourn at two different sites below a depth of approximately 15 cm. This suggests that, unlike in other systems where interstitial taxa have been found in significant abundances (Dole-Olivier *et al.* 1997; Schmid-Araya, 1997; Franken *et al.* 2001; Stead *et al.* 2004), within chalk stream ecosystems the hyporheic zone may be of limited importance.

Benthos spatial and temporal patterns

Many previous studies have noted the preferences of macroinvertebrates for macrophyte stands over gravel beds (Wright, 1984; Pinder, 1992; Wright and Symes, 1999; Harrison *et*

al. 2005). Further to this, within lentic systems a similar pattern for meiofauna has been found (Paterson, 1993; Silver & Cowell, 1993), while associations in streams and rivers with bryophytes have been made (Suren, 1992; Linhart *et al.* 2002; Fontaneto *et al.* 2005). In this study the strong association between higher plant lotic macrophytes and meiofauna has been demonstrated for the first time. The mean density and biomass of meiofauna remained consistently higher in the macrophyte stands than gravel beds over the whole one year sampling period. Furthermore, species richness varied between the two habitats, and species-abundance relationships showed a preference for macrophyte stand habitats over gravel beds for seasonally synchronised taxa. This was indicated by the greater change in composition seasonally within the macrophyte stands when compared with the gravel beds.

Stead *et al.* (2003) demonstrated a differing response of benthic macroinvertebrates and meiofauna to the same suite of environmental variables spatially and temporally. In contrast, within the River Lambourn a similar spatial pattern of distribution for both macrofauna and meiofauna was found (see Chapter 2). Interestingly, the temporal pattern of change in total density for both size classes was almost identical, with peaks in late spring to summer months. Potentially, the two size classes could be responding to different changes in environmental variables which are coincidental in timing. However, it is more likely that they are both responding to the same suite of changes brought by new growth of macrophytes, potentially increasing habitat complexity with the concomitant benefits such as improved refugia or greater food availability.

System stability

Chalk streams are predicted to be naturally highly stable relative to other lotic systems (Prenda, *et al.* 1997; Pretty *et al.* 2006). Consistent with this, species-abundance relationships for both benthic communities within the River Lambourn described in

Chapter 2 were not significantly different from log normal. Log normal distributions reflect assemblages of species which are at equilibrium. Moreover, density-size spectra in Chapter 5 showed stable bimodal distributions, temporally and spatially. In the only investigations of density-size spectra over a similar temporal and spatial scale, Stead *et al.* (2005b) found a highly variable pattern. Furthermore, Stead *et al.* (2004) proposed that meio- and macrofauna responded differently to environmental fluctuations while here a synchronised response was found possibly due to the greater stability of the River Lambourn.

Secondary production and standing biomass

Meiofauna are known to be affected detrimentally by high levels of disturbance, in particular spates in stream channels, some taxa struggling even in medium flows (Robertson, 2000). Considering the apparent stability of the biota (Chapter 2,5), and environmental conditions (Prenda, *et al.* 1997; Pretty *et al.* 2006), the results of the investigation into production and standing biomass (Chapter 3) may seem surprising. Both production and standing biomass were dominated by macroinvertebrates. High P/B ratios for many meiofauna taxa were found. However, even coupled with higher densities than those of macrofauna (Chapter 2), high P/B ratios were insufficient to compensate for the small individual biomass of meiofauna. The findings suggest meiofauna do not contribute significantly to production and standing biomass in chalk streams. Published estimates of production and standing biomass for both macrofauna and meiofauna are rare. However, Hakenkamp and Morin (2000) asserted that the importance of meiofauna will vary widely and it is likely that they have a limited role within the benthic secondary production of lotic environments, consistent with the finding reported here.

Trophic and functional role of meiofauna

The few published highly resolved food webs have generally tended to be dominated by intermediate species (Martinez, 1991; Polis, 1991; Hall and Raffaelli, 1991; Schmid-Araya *et al.* 2002a). The food webs presented here for the River Lambourn followed this pattern (Chapter 4). Meiofauna generally occupy *intermediate* positions in stream food webs (Schmid-Araya and Schmid, 2000) and therefore may perform an important trophic function, linking *basal* and *top* species in chalk streams.

Highly resolved webs are characterised by low connectance values (Schmid-Araya *et al.* 2002a), and this was also true within the River Lambourn. Low connectance is due to there being a high number of feeding interactions which are not recognised. Feeding interactions may therefore be weak, and consequently difficult to identify. Stable isotope analysis and gut content data (Chapter 4; Pretty *et al.* in press) indicated a generalist feeding of invertebrate taxa in the River Lambourn. Generalist feeding would help to explain how species can persist when they are only involved in weak interactions. Intriguingly, McArthur (1955) argued that community stability arises through population stability which should be greatest when consumers are able to rely upon a wider range of resources. Moreover, Romanuk *et al.* (2006) found a correlation between population stability of invertebrates in rock pools and diet breadth measured using stable isotopes. Consequently, the high stability of the invertebrate assemblage in the River Lambourn evidenced by the species-abundance relationships (Chapter 2), and density-size spectra (Chapter 5) may have been in some part a function of the high number of potential resources available to the invertebrate consumers.

Numerous studies have reported plasticity of feeding for freshwater invertebrates before and after Cummins (1974) formalised the concept of functional feeding groups (Slack, 1936; Feminella and Stewart, 1986; Lancaster *et al.* 2005). The gut content data

from the River Lambourn (Chapter 4) did not conform to the functional feeding group classifications. Moreover, the lack of isotopic distinction between supposed fine particle feeders and coarse particle feeders was in contrast to the original classification proposed by Cummins (1974).

Furthermore, the generalist feeding on both heterotrophic and autotrophic sources of carbon for invertebrates contradicted the analysis of Finlay (2001), where autotrophic carbon was predicted to dominate food webs in lotic systems with catchment areas greater than 10 km^2. The original Riverine Productivity Model (RPM) of Thorp and Delong (1994) most accurately depicted the River Lambourn invertebrate community. This is because the original RPM model incorporates significant inputs of both autotrophic and heterotrophic carbon to the system, which is what was found in the River Lambourn.

Meiofauna have been almost completely ignored in river models and concepts. Many of the findings presented here such as the reduced biomass and production and lack of hyporheic densities indicate a limited functional role for meiofauna in chalk stream ecosystems. However, throughout the literature instances of meiofauna feeding on bacteria, algae, detritus, diatoms, and protozoa can be found (Perlmutter and Meyer, 1991; Borchardt and Bott; 1995; Bott and Borchardt, 1999; Hall and Meyer, 1998). Within the simplified chalk stream food web, meiofauna were shown to be generalists, reflecting the results of the gut content and unique stable isotope analysis performed. Therefore, in other lotic systems where relative to macrofauna their densities and biomass may be higher, with plasticity of feeding, meiofauna may not consume resources in the same proportions as the macrofauna. In those circumstances meiofauna may play an important role in determining the heterotrophic-autotrophic balance of different lotic ecosystems, and are therefore worth further consideration in river models and concepts as they may need revising.

Density body size allometry

Makarieva *et al.* (2004) suggested that the failure of some investigations, particularly of lotic systems, to find close conformity between empirical data of density-size distributions and theoretical predictions was due to high natural levels of disturbance. Independent evidence for the view that unstable systems yield shallow density-body size exponents was found by Cyr *et al.* (1997). They measured anthropogenic disturbance on lentic communities finding shallow slopes. The lotic investigation of Stead *et al.* (2005*b*) which included meiofauna failed to find a clear density-size distribution for what appeared to be an unstable community suffering high levels of disturbance due to variable acidity providing further evidence.

The data presented here and the prevailing environmental conditions indicated that the River Lambourn was a stable system. However, density size distributions did not conform to any theoretical predictions of the metabolic theory, or the hypothesis of Makarieva *et al.* (2004) for stability. Shallower exponents than expected by metabolic theory and for stable systems were found (Chapter 5). Consequently, in this study the hypothesis of Makarieva *et al.* (2004) was rejected. Furthermore, metabolic constraints were rejected as the major factor determining energetic balances between species in the River Lambourn. There was no energy equivalence, a clear pattern in the distributions of a greater share of energy going to larger taxa was found. This pattern was consistent with the dominance of macroinvertebrates in terms of production and standing biomass (Chapter 3).

Considering the findings of Chapter 4 in which many weak trophic interactions were indicated, the high diversity of species with low abundance found in the River Lambourn (Chapter 2) seems logically consistent. Furthermore, the pyramidal shape of the food webs suggested greater functional redundancy within lower trophic levels (Chapter 4). With the size structuring of food webs (Warren and Lawton, 2004; Woodward *et al.* 2005;

Jennings *et al.* 2007), effects of trophic transfer inefficiency, and variable changes in resource availability for species of different body size due to fractal geometry, a diversity-stability-trophic structure explanation for density-body size distributions seemed most plausible.

Other allometric relationships

Benke (1993) tested the predictive model of the P/B-body size relationship and concluded it was too inaccurate to be valid. Errors of greater than 300% were not uncommon. In the analysis performed here the body size spectrum was extended over the meiofaunal size range of freshwater invertebrates for the first time. Although the P/B-body size relationship yielded an exponent close to that of theoretical predictions, correlation coefficients were generally too low to advocate any predictive powers. Furthermore, unlike Ernest *et al.* (2003) no evidence for a relationship between production and body size close to theoretical predictions of metabolic theory was found, nor indeed was there a conforming pattern for standing biomass.

Standing biomass and density exponents balanced one another as expected, while production is estimated as a product of standing biomass and density. Consequently, the diversity-stability-trophic structure theory can explain the lack of conformance to metabolic constraints for all three allometric relationships. However, P/B allometry did conform to metabolic constraints, but only for the regressions of the whole assemblages. The most parsimonious explanation for this is that species within communities may alter their metabolism up or down in relation to environmental variables but only within the physiological constraints determined by body size. Consequently, metabolism may always be able to predict some level of the variance in the distribution of energy within communities. However, if we are to understand the structure and function of real systems

then general variables such as ecosystem or community properties may be more important predictors of structure of assemblages rather than variables derived ultimately at the level of the individual.

Future directions

Specifically with regard to chalk streams, our understanding of these systems would benefit from investigations into exactly what advantages are conferred upon meiofauna from a close association with lotic macrophytes. The same could also be said for many of the macrofauna taxa which beyond descriptions of their life-history and reproduction, behavioural studies remain untouched.

Interestingly, macrophytes can be considered ecosystem engineers as they modify flow, increase organic matter and nutrient retention, and recycling (Battle and Mihuc, 2000; Wilcock *et al.* 2004; Cotton *et al.* 2006). Meiofauna may play an important functional role within the sediments of macrophyte stands improving biogeochemical cycling through actions such as bioturbation which increases pore-spaces and consequently improves fluxes of oxygen and nutrients, and through grazing on bacteria increasing their growth rates (Boulton *et al.* 2002). In marine and lentic systems the role of small invertebrates in microbial dynamics has been examined but lotic systems are yet to be extensively investigated (Hakenkamp and Palmer, 2000).

Lotic studies of whole communities including both meiofauna and macrofauna from a variety of systems are needed to assess and understand differences in the spatio-temporal dynamics of both size classes. More studies of whole invertebrate assemblages are needed to answer whether meiofauna are really limited by their small size in contributing significantly to lotic ecosystem production and standing biomass. It is also possible river models and concepts would benefit greatly from inclusion of meiofauna, but this requires a

significant research effort into their functional role in a variety of low, medium and high order systems.

Finally, our ability to make generalisations across different systems would benefit greatly from more investigations of highly resolved food webs from many different ecosystems. While more studies of allometric relationships of density, P/B, production and standing biomass are needed from real ecosystems as well. Synthesis between different disciplines within ecology may then provide more accurate insights into the interrelationships of different ecosystem properties such as structure, stability and function.

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Appendix 2. Taxon specific regression equations and parameters used to calculate biomass of invertebrates. Taxa are ordered alphabetically by author and then regression taxa used. Lambourn Taxa refers to specific taxa to which regression taxa equations were applied. (DW = dry weight, V = volume, WW = wet weight, L = body length, SL = shell length, W = body width)

Author	Taxa	Lambourn Taxa	Formula
Alvarez & Pardo (2005)	*Agapetus quadratus*	*Agapetus fuscipes*	DW µg = $7.59*Lmm^{2.9}$
Andrassy (1956)	Nematoda	Nematoda	WW µg = $L\mu m*W\ \mu m^2/1600000$
Benke, *et al.* (1999)	*Caenis spp.*	*Caenis spp.*	DW mg = $0.0069*Lmm^{2.61}$
	Chironomidae	All remaining Chironomidae species	DW mg = $0.0006*Lmm^{2.77}$
	Chironominae	All remaining Chironominae, *Paracladopelma spp.*	DW mg = $0.0059*Lmm^{2.099}$
	Elimia cahawbensis	All Gastropoda species	DW mg = $0.0331*Lmm^{2.851}$
	Ephemera spp.	*Ephemera spp.*	DW mg = $0.0021*Lmm^{2.737}$
	Ephemeroptera	All remaining Ephemeroptera species	DW mg = $0.0077*Lmm^{2.74}$
	Heptageniidae	*Heptagenia spp.*	DW mg = $0.0108*Lmm^{2.754}$
	Leptophlebidae	*Paraleptophlebia spp.*	DW mg = $0.0047*Lmm^{2.686}$
	Oecetis spp.	Leptoceridae	DW mg = $0.0034*Lmm^{3.212}$
	Orthocladiinae	All remaining Orthocladiinae, Genus *Cricotopus*, Genus *Orthocladius*, Genus *Thienemaniella*, Genus *Tvetenia*, *Brillia modesta*, *Heleniella ornatocollis*, *Paramectrocnemius stylatus*, *Paratrissocladius excerptus*, *Parorthocladius nudipennis*, *Rheocricotopus fuscipes*, *Symposiocladius lignicola*, *Synorthocladius semivirens*	DW mg = $0.002*Lmm^{2.254}$
	Pacifastacus leniusculus trowbridgii (m)	Astacidae	DW mg = $0.0084*Lmm^{3.592}$
	Polycentropus spp.	All *Polycentropus spp.*	DW mg = $0.0071*Lmm^{2.531}$
	Polypedilum spp.	All *Polypedilum spp.*	DW mg = $0.001*Lmm^{2.761}$
	Tanypodinae	All Tanypodinae species	DW mg = $0.0026*Lmm^{2.503}$
	Tanytarsus spp.	*Rheotanytarsus spp.*, *Tanytarsus spp.*	DW mg = $0.0012*Lmm^{2.294}$
	Trichoptera	Trichoptera, *Adicella filicornis*, *Athripsodes spp.*, *Chaetopteryx spp.*, *Mystacides azurea*, *Potamophylax spp.*	DW mg = $0.0056*Lmm^{2.839}$

App. 2 continued

Author	Taxa	Lambourn Taxa	Formula
Burgherr & Meyer (1997)	*Hydropsyche spp.*	All *Hydropsyche* species	DW mg = $0.001892229*Lmm^{2.89}$
	Leuctra spp.	All Plecoptera species	DW mg = $0.002198456*Lmm^{2.66}$
	Simulium spp.	All *Simulium spp.*	DW mg = $0.002908843*Lmm^{2.67}$
Dumont, *et al.* (1975)	Cyclopoida	Cyclopoida	DW µg = $1.1*10^{-7}*L\mu m^{2.59}$
	Harpacticoida	Harpacticoida	DW µg = $12.51*L\mu m^{4.4}$
Feller & Warwick (1988)	Acari	Acari	Vnl = Lmm * Wmm^2 * 399
	Tardigrada	Tardigrada	Vnl = Lmm * Wmm^2 * 614
	Turbellaria	All Microturbellaria	Vnl = Lmm * Wmm^2 * 550
Finogenova (1984)	Naididae	Oligochaeta	WW mg = $0.0035*Lmm^{2.1}$
Herzig (1984)	*Alona spp.*	Cladocera	DW µg = $6*Lmm^{2.653}$
Johnston & Cunjak (1999)	*Micropsectra spp.*	*Micropsectra spp.*	DW mg = $0.000662*Lmm^{2.59}$
	Corynoneura lobata	All *Corynoneura* species	DW mg = $0.00147*Lmm^{2.1}$
	Eukiefferiella brehmi/ gracei group	All *Eukiefferiella* species	DW mg = $0.00201*Lmm^{2.24}$
Meyer (1989)	*Ancylus fluviatillis*	*Ancylus fluviatillis*	DW mg = $0.035725163*SLmm^{3.14}$
	Baetis rhodani	*Baetis rhodani*	DW mg = $0.002385134*Lmm^{3.115}$
	Drusinae	*Drusus annulatus*	DW mg = $0.007531207*Lmm^{2.925}$
	Elmis spp.	*Elmis spp.*	DW mg = $0.014641431*Lmm^{2.459}$
	Goeridae	Goera *spp., Silo spp.*	DW mg = $0.001566988*Lmm^{4.244}$
	Limnephilidae	*Limnephilus spp.*	DW mg = $0.00541328*Lmm^{2.966}$
	Psychomyidae	*Psychomia pusilla, Psychomia spp.*	DW mg = $0.001824408*Lmm^{3.129}$

App. 2 continued

Author	Taxa	Lambourn Taxa	Formula
	Rhyacophila spp.	All *Rhyacophila* species	DW mg = $0.001593376*Lmm^{3.123}$
	Sericostoma spp.	All *Sericostoma* species	DW mg = $0.011378838*Lmm^{2.649}$
	Serratella ignita	*Serratella ignita*	DW mg = $0.005403005*Lmm^{3.057}$
Nolte (1990)	*Diamesa spp.*	*Potthastia longimana, Prodiamesa olivacea*	DW mg = $0.001967483*Lmm^{2.602}$
Poepperl (1998)	Ceratopogonidae	Ceratopogonidae	DW mg = $0.002*Lmm^{2.438}$
	Erpobdella octoculata	*Erpobdella octoculata*	DW mg = $0.0058*Lmm^{2.225}$
	Gammarus pulex	*Gammarus pulex*	DW mg = $0.0019*Lmm^{2.964}$
	Glossiphonia complanata	*Glossiphonia complanata, G. heteroclita, Piscicola geometra, Theromyzon tessulatum*	DW mg = $0.0198*Lmm^{2.212}$
	Helobdella stagnalis	*Haemopsis sanguisinga*	DW mg = $0.0294*Lmm^{1.752}$
	Limoniidae	Limoniinae	DW mg = $0.0039*Lmm^{2.44}$
Reiss (2006)	Rotifera	All Rotifera	$Vml = (L\mu m * W\mu m^2 * 3.14)/6$
Schmid-Araya, unpublished	Ostracoda	Ostracoda	DW µg = $0.00000007*Lmm^{1.943}$

Appendix 3. List of species found in surface and subsurface samples taken from the River Lambourn from April 2004 to March 2005.

Taxa	Surf.	Subs.	Taxa	Surf.	Subs.
Arachnida			Chironomidae		
Acari sp.	+	+	*Apsectrotanypus spp.*	+	-
Crustacea			*Brillia modesta* Meigen	+	-
Astacidae			Chironomid sp.	+	+
Astacidae Genus sp.	+	-	Chironominae sp.	+	-
Cladocera			*Conchapelopia spp.*	+	-
Alona rustica T.Scott	+	+	*Corynoneura spp.*	+	-
Gammaridae			*Corynoneura coronata* Edwards	+	-
Gammarus pulex (L.)	+	+	*Corynoneura lobata* Edwards	+	-
Niphargus fontanus Bate	-	+	*Corynoneura sp. A.*	+	-
Copepoda			*Cricotopus bicinctus* (Meigen)	+	-
Cyclopoida			*Cricotopus brevipalpis* Kieffer	+	-
Cyclopoida Genus sp.	+	+	*Cricotopus spp.*	+	-
Harpacticoida			Diamesinae sp.	+	-
Bryocamptus cuspidatus (Schmeil)	+	+	*Eukiefferiella gracei* (Edwards)	+	-
Bryocamptus echinatus (Mrázek)	+	+	*Eukiefferiella brevicalcar* (Kieffer)	+	-
Bryocamptus pygmaeus (Sars)	+	+	*Eukiefferiella claripennis* (Lundbeck)	+	-
Bryocamptus vejdovski	+	+	*Eukiefferiella clypeata* (Kieffer)	+	-
Paracamptus schmeili (Schmeil)	+	+	*Eukiefferiella coerulescens* (Kieffer)	+	-
Ostracoda			*Eukiefferiella ilkleyensis* (Edwards)	+	-
Ostracoda Genus sp.	+	+	*Eukiefferiella lobifera* Goetghebuer	+	-
Insecta			*Eukiefferiella sp. 1.*	+	-
Coleoptera			*Eukiefferiella spp.*	+	-
Elmidae			*Heleniella ornaticollis* (Edwards)	+	+
Elmis aenea (Müller)	+	-	*Macropelopia spp.*	+	-
Elmis sp. B.	+	-	*Micropsectra spp.*	+	-
Elmis sp.	+	-	Orthocladiinae sp.	+	+
Diptera			*Orthocladius (O.) sp D.*	+	-
Ceratopogonidae			*Orthocladius excavatus* Brundin	+	-
Ceratopogonidae Genus. sp.	+	+	*Orthocladius rivulorum* Kieffer	+	-
			Orthocladius sp. B.	+	-

App. 3 continued

Taxa	Surf.	Subs.	Taxa	Surf.	Subs.
Chironomidae cont.			Simuliidae		
Orthocladius sp.1.	+	-	*Simulium spp.*	+	+
Orthocladius spp.	+	-	Limoniidae		
Orthocladius thienemanni Kieffer	+	-	Limoniinae Genus sp.	+	+
Orthocladius wetterensis Brundin	+	-	Ephemeroptera		
Paracladopelma spp.	+	-	*Baetis rhodani* (Pictet)	+	-
Paramectriocnemus stylatus Kieffer	+	-	*Baetis spp.*	+	-
Paratrissocladius excerptus (Walker)	+	-	*Caenis rivulorum* Eaton	+	-
Polypedilum c.f. laetum (Meigen)	+	-	*Caenis spp.*	+	-
Polypedilum cultellatum Goetghebuer	+	-	*Ephemera danica* Müller	+	-
Polypedilum spp.	+	-	*Ephemera spp.*	+	-
Potthastia longimana Kieffer	+	-	*Heptagenia spp.*	+	-
Prodiamesa olivacea (Meigen)	+	-	*Heptagenia sulphurea* (Müller)	+	-
Rheocricotopus fuscipes (Kieffer)	+	-	*Paraleptophlebia spp.*	+	-
Rheotanytarsus sp.	+	+	*Serratella ignita* (Poda)	+	-
Symposiocladius lignicola (Kieffer)	+	-	Plecoptera		
Synorthocladius semivirens Kieffer	+	-	*Leuctra fusca* (L.)	+	-
Tanypod spp.	+	-	*Leuctra spp.*	+	-
Tanytarsus spp.	+	-	Trichoptera		
Thienemaniella clavicornis (Kieffer)	+	-	*Adicella filicornis* (Pictet)	+	-
Thienemaniella majuscula (Edwards)	+	-	*Agapetus fuscipes* Curtis	+	-
Thienemaniella partita Shlee	+	-	*Agapetus spp.*	+	-
Thienemaniella sp.E.	+	-	*Athripsodes albifrons* (L.)	+	-
Thienemaniella sp.	+	-	*Athripsodes spp.*	+	-
Thienemaniella vittata Edwards	+	-	*Chaetopteryx spp.*	+	-
Tvetenia bavarica cf	+	-	*Chaetopteryx villosa* (Fabricius)	+	-
Tvetenia calvescens (Edwards)	+	-	*Drusus annulatus* (Stephens)	+	-
Tvetenia discoloripes/veralli	+	-	Goerid sp.	+	-
Tvetenia sp. A.	+	-	*Hydropsyche pellucidula* (Curtis)	+	-
Tvetenia spp.	+	-	*Hydropsyche siltalai* Döhler	+	-
			Leptocerid sp.	+	-

App. 3 continued

Taxa	Surf.	Subs.	Taxa	Surf.	Subs.
Trichoptera cont.			*Glossiphonia heteroclite* (L.)	+	-
Limnephilus lunatus (Curtis)	+	-	*Haemopsis sanguisinga*	+	-
Limnephilus spp.	+	-	*Phagocata vitta* (Dugés)	+	-
Lype reducta (Hagen)	+	-	*Piscicola geometra* (L.)	+	-
Metalype fragilis (Pictet)	+	-	*Theromyzon tessulatum* (Miller)	+	-
Mystacides azurea (L.)	+	-	Micrognathozoa		
Polycentropus flavomaculatus (Pictet)	+	-	*Limnognathia spp.*	-	+
Polycentropus spp.	+	-	Nematoda		
Potamophylax latipennis (Curtis)	+	-	Nematoda Genus sp.	+	+
Psychomia pusilla (Fabricius)	+	-	Oligochaeta		
Psychomyiid spp.	+	-	*Aelosoma spp.*	+	-
Rhyacophila dorsalis (Curtis)	+	-	*Aelosoma hemprichi* (Ehrb.)	+	-
Rhyacophila septentrionis (McLachlan)	+	-	*Cernosvistoviella*	+	-
Rhyacophila spp.	+	-	*Chaetogaster spp.*	+	+
Sericostoma personatum (Kirby & Spence)	+	-	*Chaetogaster langi* Bretscher	+	-
Sericostoma spp.	+	-	*Eisenniella spp.*	+	-
Silo nigricornis (Pictet)	+	-	*Haplotaxis gordioides* (Hartmann)	+	-
Silo spp.	+	-	*Henlea spp.*	+	-
Gastropoda			*Homochaeta naidina* Bretscher	+	+
Ancylus fluviatillis (Müller)	+	-	Lumbricidae Genus sp.	+	+
Potamopyrgus antipodarum (Gray)	+	-	Lumbriculidae Genus sp.	+	+
Viviparus spp.	+	-	*Lumbriculus variegates* (Müller)	+	+
Pisidium Genus sp.	+	-	*Marionina spp.*	+	-
Planorbis spp.	+	-	*Nais pardalis* Piguet	+	-
Gastrotricha			*Nais simplex* Piguet	+	-
Gastrotricha sp.	+	+	*Potamothrix bavaricus* (Oschmann)	+	-
Macrodasyida sp.	-	+	*Pristina spp.*	+	-
Chaetonotus spp.	+	+	*Psammoryctides barbatus* (Grube)	+	-
Hirudinea			*Stylodrilus spp.*	+	-
Erpobdella octoculata (L.)	+	-	*Stylodrilus heringianus* (Claparede)	+	-
Glossiphonia complanata (L.)	+	-	*Stylaria lacustris* (L.)	+	-

App. 3 continued

Taxa	Surf.	Subs.
Rotifera		
Adineta spp.	-	+
Cephalodella gibba (Ehrb.)	+	+
Cephalodella megalocephala (Glasscott)	+	-
Colurella geophila Donner	+	-
Colurella hindenbergi Steinecke	+	-
Colurella spp.	+	+
Dicranophorus lutkenyi	+	+
Dicranophorus secretus Donner	-	+
Dicranophorus spp.	-	+
Dicranophorus uncinatus (Milne)	-	+
Dissotrocha macrostyla (Ehrb.)	+	+
Embata laticeps (Murray)	-	+
Embata spp.	+	-
Encentrum spp.	+	-
Euchlanis spp.	+	+
Lepadella quadricarinata (Stenroos)	+	-
Notholca squamula Müller	+	-
Philodina flaviceps Bryce	+	-
Philodina spp.	-	+
Proales globulifera (Hauer)	-	+
Proales theodora (Gosse)	+	-
Resticula spp.	-	+
Rotaria neptunoidea (Harring)	+	-
Rotaria rotatoria (Pallas)	+	+
Rotaria spp.	-	+
Wierzejskiella velox (Wiszniewski)	-	+
Tardigrada		
Tardigrada Genus sp.	+	-
Macrobiotus sp.	+	+

Taxa	Surf.	Subs.
Turbellaria		
Geocentrophora baltica (Kennel)	+	-
Gyratrix hermaphroditus Ehrenberg	+	-
Gyratrix spp.	-	+
Limnoruanis romanae Kolasa	+	-
Macrostomum johni Young	-	+
Macrostomum rostratum (Papi)	+	+
Macrostomum spp.	+	+
Macrostomum tuba (von Graff)	+	-
Macrodalyellia spp.	-	+
Microturbellaria Genus sp.	+	+
Opisthocystis goettei (Bresslau)	+	-
Polycelis felina (Dalyell)	-	+
Polycelis tenuis (Ijima)	+	+
Prorhynchus stagnalis M. Schultze	+	-
Rhyncoscolex simplex Leidy	+	+
Stenostomum anatirostrum Marcus	-	+
Stenostomum grabbkoense	+	+
Stenostomum spp.	+	+
Stenostomum unicolor Schmidt	+	-
Total Species	185	57

Appendix 4. Published minimum and maximum generation times, and mean flight periods where applicable, in days (d), for various taxonomic groups and Lambourn taxa to which literature data were applied with references.

Literature taxa	Lambourn taxa	Generation time (d) Min	Max	Av. flight per. (d)	Reference
Acari					
Acari	Acari	42	730	n/a	Di Sabatino *et al.* (2000)
Ceratopogonidae					
Ceratopogonidae	Ceratopogonidae	365	365	<7	Stead *et al.* (2005a)
Chironomidae					
Tanypodinae, *Apsectrotanypus trifascipennis*	Tanypodinae, *Apsectrotanypus, Conchapelopia, Macropelopia*	183	365	<7	Stead *et al.* (2005a); Hildrew *et al.* (1985); Lindegaard and Mortensen (1988); Pers. obs.
Stempellinella	*Brillia modesta*	183	183	<7	Stead *et al.* (2005a)
Eukiefferiella, Corynoneura, Prodiamesa, Apsectrotanypus	Chironomidae, Orthocladiinae, *Thienemaniella* spp., *Tvetenia* spp., Symposiocladius lignicola	120	365	<7	Stead *et al.* (2005a); Lindegaard and Mortensen (1988)
Chironominae	Chironominae	120	365	<7	
Corynoneura lobata	*Corynoneura* spp.	120	120	<7	Stead *et al.* (2005a)
Eukiefferiella	*Eukiefferiella* spp.	120	120	<7	Berg and Hellenthal (1992)
Macropelopia sp.	*Macropelopia* sp.	183	365	<7	Stead *et al.* (2005a)
Micropsectra spp.	*Micropsectra* sp.	197	197	<7	Lindegaard and Mortensen (1988)
Orthocladius spp.	*Orthocladius* spp.	365	365	<7	Pers. obs.
Polypedilum sp.	*Paracladopelma, Polypedilum* spp.	60	358	<7	Stead *et al.* (2005a)

App. 4 continued

Orthocladius spp., *Paramectriocnemus stylatus*, *Paratrissocladius excerptus*, *Parorthocladius nudipennis*, *Potthastia longimana*, *Prodiamesa olivacea*, *Rheocricotopus fuscipes*, *Synorthocladius semivirens*	*Orthocladius spp.*, *Paramectriocnemus stylatus*, *Paratrissocladius excerptus*, *Parorthocladius nudipennis*, *Potthastia longimana*, *Prodiamesa olivacea*, *Rheocricotopus fuscipes*, *Synorthocladius semivirens*	358	358	<7	Pers. obs.
Heterotrissocladius marcidus	*Rheotanytarsus*, *Tanytarsus*	176	176	<7	Hildrew and Townsend (1982), Pers. obs.
Cladocera					
Alona costata	Cladocera	140	140	n/a	Dole-Olivier *et al.* (2000)
Copepoda					
Megacyclops viridis viridis	Cyclopoida	90	183	n/a	Dole-Olivier *et al.* (2000)
Bryocamptus zschokkei	Harpacticoida	153	336	n/a	Dole-Olivier *et al.* (2000)
Coleoptera					
Elmis spp.	*Elmis* spp.	365	365	n/a	Elliot (2006)
Ephemeroptera					
Caenis spp.	*Caenis* spp.	365	365	24.5	Stead *et al.* (2005a)
Baetis rhodani	*Baetis* spp.	61	152	n/a	Elliot and Humpesch (1983)
Ephemera spp.	*Ephemera* spp.	730	1095	n/a	Elliot and Humpesch (1983)
Serratella ignita	*Serratella ignita*	152	152	n/a	Elliot and Humpesch (1983)
Heptagenia spp.	*Heptagenia* spp.	365	365	n/a	Elliot and Humpesch (1983)
Paraleptophlebia spp.	*Paraleptophlebia* spp.	213	365	n/a	Elliot and Humpesch (1983)
Gammaridae					
Gammarus pulex	*Gammarus pulex*	700	730	n/a	Welton (1979)
Gastrotricha					
Gastrotricha	Gastrotricha	15	20	n/a	Ricci and Balsamo (2000)
Microturbellaria					
Microturbellaria	Microturbellaria	7	49	n/a	Kolasa (2000)

App. 4 continued

Gastropoda					
Ancylus fluviatillis	*Ancylus fluviatillis*	365	730	n/a	Geldiay (1956), Thorup (1963)
Potamopyrgus antipodarum	*Potamopyrgus antipodarum*, Gastropoda, *Planorbis* sp.	122	213	n/a	Frömming (1956)
Hirunidae					
Erpobdella octoculata	*Erpobdella octoculata*	365	1095	n/a	Elliot and Mann (1998)
Glossiphonia heteroclita	Glossiphonia heteroclita	122	487	n/a	Elliot and Mann (1998)
Glossiphonia complanata	Glossiphonia complanata	365	1095	n/a	Elliot and Mann (1998)
Haemopsis sanguisinga	Haemopsis sanguisinga	365	365	n/a	Elliot and Mann (1998)
Theromyzon tessulatum	Theromyzon tessulatum	365	365	n/a	Elliot and Mann (1998)
Piscicola geometra	Piscicola geometra	365	365	n/a	Elliot and Mann (1998)
Nematoda					
Nematoda	Nematoda	13	365	n/a	Traunspurger (2000)
Oligochaeta					
Oligochaeta	Oligochaeta	365	365	n/a	Learner *et al.* (1978), Morgan *et al.* (1980)
Ostracoda					
Notodromas monacha	Ostracoda	21	35	n/a	Dole-Olivier *et al.* (2000)
Plecoptera					
Leuctridae	Plecoptera, Leuctridae	365	548	n/a	Stead *et al.* (2005a)
Rotifera					
Bdelloidea	Bdelloidea	30	40	n/a	Ricci and Balsamo (2000)
Monogononta	Monogononta	7	10	n/a	Ricci and Balsamo (2000)
Simuliidae					
Simuliidae	*Simulium* spp.	122	365	17.5	Waters (1977)
Tardigrada					
Tardigrada	Tardigrada	91	913	n/a	Nelson and Marley (2000)
Tipulidae					
Tipulidae	Limoniinae	365	365	<7	Waters (1977)

App. 4 continued

Trichoptera					
Agapetus spp.	*Agapetus* spp.	365	365	n/a	Pers. obs.
Athripsodes aterrimus	*Athripsodes* spp., Leptocerid sp., *Mystacides azurea*	365	365	24.5	Morgan (1956)
Chaetopteryx villosa	*Chaetopteryx* spp.	365	365	24.5	Andersen and Tysse (1984), Elliot (1971)
Drusus annulatus	*Drusus annulatus*	365	365	24.5	Elliot (1971)
Silo nigricornis	*Goerid* spp., *Silo nigricornis*, *Silo* sp.	365	365	24.5	Nielsen (1942)
Hydropsyche pellucidula	*Hydropsyche pellucidula*	365	365	24.5	Edington and Hildrew (1995)
Hydropsyche siltalai	*Hydropsyche siltalai*	365	365	24.5	Edington and Hildrew (1995)
Limnephilus lunatus	*Limnephilus* spp.	365	365	24.5	Gower (1967)
Cyrnus trimaculatus	*Lype reducta*	365	365	24.5	Waters (1977)
Polycentropus flavomaculatus	*Polycentropus* sp.	365	730	n/a	Elliot (1968)
Potamophylax cingulatus	*Potamophylax* sp.	365	365	24.5	Waters (1977)
Psychomyiid spp.	*Psychomia pusilla*, Psychomyiid sp.	365	365	24.5	Edington and Hildrew (1995)
Rhyacophila dorsalis	*Rhyacophila* sp., *R. dorsalis*, *R. septentrionis*	365	456	n/a	Elliot (1968)
Sericostoma personatum	*Sericostoma* sp., *S. personatum*	365	1095	n/a	Elliot (1969)

Appendix 5. Minimum and maximum cohort production intervals, production values, and P/B ratios for taxonomic groups found within macrophyte stands.

Group	CPI		Production ($g\ m^{-2}\ yr^{-1}$)		Biomass ($g\ m^{-2}$)	P/B	
	Min	Max	Min	Max		Min	Max
Acari	42	730	0.02	0.32	0.01	2.61	45.22
Astacidae	36500	4380	0.08	0.1	0.15	0.53	0.63
Ceratopogonidae	358	358	0.09	0.09	0.02	4.06	4.06
Chironomidae							
Apsectrotanypus	176	358	0.01	0.02	0.003	3.62	7.37
Brillia modesta	176	176	0.03	0.03	0.003	7.82	7.82
Chironomidae	113	358	0.001	0.004	0.0002	5.12	16.23
Chironominae	113	358	0.03	0.09	0.01	3.51	11.13
Conchapelopia	176	358	0.04	0.08	0.01	4.12	8.39
Corynoneura coronata	113	113	0.00002	0.00002	0.00001	2.61	2.61
Corynoneura lobata	113	113	0.01	0.01	0.001	8.93	8.93
Corynoneura	113	113	0.003	0.003	0.0001	17.14	17.14
Corynoneura sp. A	113	113	0.00003	0.00003	0.00001	1.86	1.86
Cricotopus bicinctus	358	358	0.004	0.004	0.001	3.68	3.68
Cricotopus brevipalpis	358	358	0.001	0.001	0.0002	3.54	3.54
Cricotopus	176	358	0.001	0.003	0.0004	3.7	7.54
Eukiefferiella brevicalcar	113	113	0.002	0.002	0.0001	14.45	14.45
Eukiefferiella claripennis	113	113	0.003	0.003	0.0002	19.34	19.34
Eukiefferiella clypeata	113	113	0.002	0.002	0.0001	17.28	17.28
Eukiefferiella coerulescens	113	113	0.02	0.02	0.001	15.47	15.47
Eukiefferiella gracei	113	113	0.001	0.001	0.00005	16.12	16.12
Eukiefferiella ilkleyensis	113	113	0.02	0.02	0.001	18.29	18.29
Eukiefferiella lobifera	113	113	0.01	0.01	0.001	21.53	21.53
Eukiefferiella sp. 1	113	113	0.001	0.001	0.0001	11.14	11.14
Eukiefferiella	113	113	0.01	0.01	0.0004	23.62	23.62
Heleniella ornatocollis	358	358	0.09	0.09	0.01	9.36	9.36
Macropelopia	176	358	0.02	0.04	0.003	5.08	10.34
Micropsectra	190	190	0.01	0.01	0.001	9.04	9.04
Orthocladiinae	113	358	0.01	0.02	0.001	4.42	14
Orthocladius excavatus	358	358	0.01	0.01	0.004	4.02	4.02
Orthocladius rivulorum	358	358	0.0004	0.0004	0.0001	3.54	3.54
Orthocladius	358	358	0.004	0.004	0.001	4.01	4.01
Orthocladius sp. 1	358	358	0.00002	0.00002	3E-07	65.75	65.75
Orthocladius sp. B.	358	358	0.01	0.01	0.0005	10.41	10.41
Orthocladius thienemanni	358	358	0.002	0.002	0.0004	3.95	3.95
Orthocladius wetterensis	358	358	0.003	0.003	0.001	4.07	4.07
Paracladopelma	53	176	0.001	0.004	0.0001	12.46	41.36
Paratrissocladius excerptus	358	358	0.01	0.01	0.004	3.33	3.33
Parorthocladius nudipennis	358	358	0.001	0.001	0.0001	12.79	12.79
Polypedilum cultellatum	53	176	0.08	0.27	0.01	9.18	30.48
Polypedilum laetum	53	176	0.001	0.005	0.0002	8.86	29.41
Polypedilum	53	176	0.01	0.02	0.001	10.49	34.84

App. 5 continued

Prodiamesa olivacea	358	358	0.03	0.03	0.01	2.68	2.68
Rheocricotopus fuscipes	358	358	0.003	0.003	0.001	4.07	4.07
Rheotanytarsus	176	176	0.1	0.1	0.01	13.54	13.54
Symposiocladius lignicola	113	358	0.0002	0.001	0.00003	6.59	20.89
Tanypodinae	176	358	0.004	0.01	0.001	5.39	10.96
Tanytarsus	176	176	0.001	0.001	0.0001	11.51	11.51
Thienemaniella clavicornis	113	358	0.004	0.01	0.001	6.65	21.08
Thienemaniella majuscula	113	358	0.001	0.002	0.0001	7.88	24.96
Thienemaniella partita	113	358	0.001	0.002	0.0001	8.199	25.98
Thienemaniella	113	358	0.02	0.05	0.001	10.67	33.79
Thienemaniella sp. E.	113	358	0.0004	0.001	0.00005	7.708	24.42
Thienemaniella vittata	113	358	0.04	0.11	0.003	12.99	41.16
Tvetenia calvescens	113	358	0.01	0.03	0.002	6.28	19.9
Tvetenia discoloripes/veralli	113	358	0.03	0.09	0.01	4.07	12.9
Tvetenia	113	358	0.002	0.01	0.0003	8.64	27.38
Tvetenia sp. A.	113	358	0.001	0.003	0.0003	3.49	11.05
Cladocera	140	140	0.66	0.66	0.01	56.46	56.46
Copepoda							
Harpacticoida	136	321	0.11	0.27	0.02	7.56	17.84
Cyclopoida	76	166	0.004	0.01	0.0004	10.81	23.3
Elmis	365	365	0.31	0.31	0.06	5.54	5.54
Ephemeroptera							
Baetis rhodani	152	182.5	0.49	1.24	0.04	13.06	32.64
Caenis	335	335	0.02	0.02	0.01	2.92	2.92
Ephemera	1095	730	0.07	0.1	0.03	2.43	3.64
Ephemeroptera	340.5	340.5	0.02	0.02	0.002	7.22	7.22
Paraleptophlebia	188	340.5	0.01	0.03	0.002	6.91	12.51
Gammarus pulex	700	730	13.83	14.42	4.12	3.35	3.5
Gastropoda							
Ancylus fluviatillis	365	730	0.22	0.45	0.11	2.01	4.02
Gastropod	122	213	0.37	0.66	0.04	9.45	16.54
Planorbis	122	213	0.19	0.34	0.02	10.44	18.27
Potamopyrgus antipodarum	122	213	8.94	15.65	1.26	7.07	12.38
Viviparus	122	213	0.02	0.04	0.002	11	19.25
Hirudinea							
Erpobdella octoculata	365	1095	0.001	0.004	0.001	0.99	2.97
Glossiphonia complanata	365	1095	0.02	0.05	0.01	1.78	5.33
Glossiphonia heteroclita	121.7	486.7	0.003	0.01	0.002	1.34	3.02
Haemopsis sanguisinga	365	365	0.04	0.04	0.02	2.67	2.67
Piscicola geometra	365	365	0.06	0.06	0.01	4.7	4.7
Theromyzon tessulatum	365	365	0.07	0.07	0.01	4.53	4.53
Limoniidae	365	365	5.49	5.49	0.89	6.14	6.14
Microturbellaria							
Geocentrophora baltica	7	49	0.001	0.004	0.0002	3.31	23.17
Gyratrix hermaphroditus	7	49	0.003	0.02	0.0001	23.5	164.47
Macrodalyellia	7	49	0.0002	0.002	0.00001	21.28	148.98

App. 5 continued

Macrostomum	7	49	0.0001	0.001	0.00001	14.18	99.28
Macrostomum tuba	7	49	0.0003	0.002	0.00002	16.55	115.87
Prorhynchus stagnalis	7	49	0.001	0.01	0.0001	9.93	69.52
Stenostomum grabbkoense	7	49	0.001	0.01	0.00004	16.55	115.87
Stenostomum	7	49	0.0004	0.003	0.00002	21.04	147.26
Nematoda	90	365	0.56	2.25	0.06	8.96	36.33
Oligochaeta	365	365	2.78	2.78	0.24	11.67	11.67
Ostracod	21	35	0.0003	0.001	0.00004	9.73	16.21
Plecoptera							
Leuctra	333.5	516	0.001	0.001	0.0002	4.44	6.87
Plecoptera	333.5	516	0.004	0.01	0.001	4.46	6.89
Rotifera							
Colurella	7	10	0.0003	0.0004	0.000003	121.67	173.81
Dicranophorus lutkenyi	7	10	0.003	0.005	0.00004	83.01	118.58
Euchlanis	30	40	0.0002	0.0003	0.00001	20.28	27.04
Philodina flaviceps	30	40	0.0002	0.0003	0.00002	14.04	18.72
Proales theodora	7	10	0.002	0.002	0.00001	146	208.57
Rotaria neptunoidea	30	40	0.0004	0.001	0.00002	20.28	27.04
Simuliidae	104.2	347.5	3.35	11.19	0.53	6.35	21.16
Tardigrada	91.25	912.5	0.0001	0.001	0.0001	1.48	14.77
Trichoptera							
Adicella filicornis	340.5	340.5	0.05	0.05	0.01	5.85	5.85
Agapetus	340.5	365	1.03	1.1	0.17	5.9	6.33
Athripsodes	340.5	340.5	0.02	0.02	0.004	5.58	5.58
Chaetopteryx	340.5	340.5	0.09	0.09	0.02	3.59	3.59
Drusus annulatus	340.5	340.5	0.03	0.03	0.004	9.18	9.18
Goerid	340.5	340.5	0.03	0.03	0.002	15.13	15.13
Hydropsyche siltalai	340.5	340.5	0.05	0.05	0.01	3.66	3.66
Leptocerid	340.5	340.5	0.04	0.04	0.01	4.13	4.13
Limnephilus	340.5	340.5	12.79	12.79	3.44	3.72	3.72
Lype reducta	340.5	340.5	0.01	0.01	0.002	6.82	6.82
Metalype fragilis	340.5	340.5	0.01	0.01	0.002	6.82	6.82
Mystacides azurea	340.5	340.5	0.04	0.04	0.01	6.7	6.7
Polycentropus	365	730	0.01	0.01	0.002	2.54	5.09
Potamophylax	340.5	340.5	0.27	0.27	0.06	4.39	4.39
Psychomia	340.5	340.5	0.01	0.01	0.001	8.6	8.6
Rhyacophila	365	456.3	0.19	0.24	0.05	3.51	4.38
Sericostoma	365	1095	0.07	0.22	0.06	1.2	3.59
Serratella ignita	152	152	1.29	1.29	0.12	10.91	10.91
Silo	340.5	340.5	0.54	0.54	0.1	5.39	5.39
Trichoptera	342.5	342.5	0.003	0.003	0.001	5.49	5.49

Appendix 6. Minimum and maximum cohort production intervals, production values, and P/B ratios for taxonomic groups found within gravel beds.

Group	CPI		Production ($g\ m^{-2}\ yr^{-1}$)		Biomass ($g\ m^{-2}$)	P/B	
	Min	Max	Min	Max		Min	Max
Acari	42	730	0.003	0.06	0.001	4.8	83.22
Astacidae	36500	4380	0.05	0.05	0.13	0.36	0.43
Ceratopogonidae	358	358	0.04	0.04	0.01	4.05	4.05
Cladocera	140	140	0.005	0.005	0.0001	32.09	32.09
Copepoda							
Cyclopoida	76	166	0.001	0.002	0.0001	10.88	23.44
Harpacticoida	136	321	0.09	0.2	0.01	8.02	18.93
Chironomidae							
Brillia modesta	176	176	0.001	0.001	0.0002	8.15	8.15
Chironomidae	113	358	0.001	0.003	0.0001	6.47	20.5
Chironominae	113	358	0.005	0.02	0.0004	11.63	36.83
Conchapelopia	176	358	0.04	0.08	0.004	8.79	17.88
Corynoneura lobata	113	113	0.01	0.01	0.0004	18.18	18.18
Corynoneura	113	113	0.002	0.002	0.001	2.58	2.58
Corynoneura sp. A.	113	113	0.001	0.001	0.0001	3.6	3.6
Potthastia longimana	358	358	0.001	0.001	0.0002	4.1	4.1
Eukiefferiella clypeata	113	113	0.003	0.003	0.0002	20.28	20.28
Eukiefferiella coerulescens	113	113	0.004	0.004	0.0002	28.03	28.03
Eukiefferiella ilkleyensis	113	113	0.002	0.002	0.0001	20.76	20.76
Eukiefferiella lobifera	113	113	0.003	0.003	0.0002	18.38	18.38
Eukiefferiella	113	113	0.01	0.01	0.0004	15.88	15.88
Heleniella ornatocollis	358	358	0.07	0.07	0.01	9.3	9.3
Micropsectra	190	190	0.001	0.001	0.0001	6.65	6.65
Orthocladiinae	113	358	0.01	0.03	0.002	4.5	14.27
Orthocladius	358	358	0.005	0.005	0.001	7.89	7.89
Orthocladius excavatus	358	358	0.001	0.001	0.0003	4.22	4.22
Orthocladius sp. D	358	358	0.0004	0.0004	0.0001	5.9	5.9
Orthocladius thienemanni	358	358	0.001	0.001	0.0003	3.81	3.81
Orthocladius wetterensis	358	358	0.003	0.003	0.001	3.84	3.84
Paracladopelma	53	176	0.003	0.01	0.0003	8.94	29.68
Paramectriocnemus stylatus	358	358	0.0003	0.0003	0.0001	3.54	3.54
Parorthocladius nudipennis	358	358	0.001	0.001	0.00004	12.79	12.79
Polypedilum cultellatum	53	176	0.03	0.09	0.002	11.58	38.45
Rheotanytarsus	176	176	0.01	0.01	0.0004	13.57	13.57
Synorthocladius semivirens	358	358	0.001	0.001	0.0001	6.59	6.59
Thienemaniella clavicornis	113	358	0.001	0.002	0.01	12.79	40.51
Thienemaniella partita	113	358	0.0001	0.0003	0.00001	9.271	29.37
Thienemaniella	113	358	0.04	0.12	0.01	3.32	10.52
Tvetenia bavarica	113	358	0.0001	0.0004	0.00002	6.59	20.89
Tvetenia calvescens	113	358	0.001	0.004	0.0002	6	19.01
Tvetenia discoloripes/veralli	113	358	0.0003	0.001	0.0001	4.92	15.59
Tvetenia	113	358	0.002	0.01	0.001	4.98	15.77
Elmis	365	365	0.08	0.08	0.02	5.11	5.11

App. 6 continued

Ephemeroptera							
Baetis rhodani	152	182.5	0.38	0.95	0.02	15.61	39.02
Caenis	335	335	0.02	0.02	0.01	2.91	2.91
Ephemera	1095	730	0.01	0.01	0.01	1.52	2.28
Ephemeroptera	340.5	340.5	0.02	0.02	0.003	6.53	6.53
Heptagenia	340.5	340.5	0.01	0.01	0.002	7.35	7.35
Serratella ignita	152	152	0.3	0.3	0.03	11.9	11.9
Gammarus pulex	700	730	4.55	4.75	1.26	3.61	3.77
Gastropoda							
Ancylus fluviatillis	365	730	0.12	0.25	0.06	2.24	4.48
Gastropod	122	213	0.12	0.2	0.01	8.73	15.28
Potamopyrgus antipodarum	122	213	3.86	6.75	0.52	7.39	12.93
Gastrotricha	15	20	0.00004	0.0001	0.000001	35.32	47.1
Hirudinea							
Glossiphonia complanata	365	1095	0.002	0.01	0.001	1.64	4.93
Haemopsis sanguisinga	365	365	0.03	0.03	0.01	2.52	2.52
Piscicola geometra	365	365	0.003	0.003	0.0004	8.91	8.91
Limoniidae	365	365	3.11	3.11	2.21	1.41	1.41
Microturbellaria							
Geocentrophora baltica	7	49	0.0002	0.001	0.00002	9.93	69.52
Gyratrix hermaphroditus	7	49	0.01	0.1	0.001	11.46	80.22
Limnoruanis romanae	7	49	0.0002	0.002	0.00005	5.14	35.96
Macrodalyellia	7	49	0.0001	0.001	0.00004	3.63	25.44
Macrostomum rostratum	7	49	0.003	0.02	0.0002	17.17	120.16
Macrostomum	7	49	0.0004	0.003	0.0001	3.17	22.19
Opisthocystis goettei	7	49	0.0002	0.001	0.00002	13.54	94.81
Prorhynchus stagnalis	7	49	0.002	0.01	0.0003	6.62	46.35
Rhyncoscolex simplex	7	49	0.01	0.05	0.0003	23.66	165.6
Stenostomum grabbkoense	7	49	0.002	0.01	0.0001	14.76	103.34
Stenostomum	7	49	0.001	0.005	0.00003	20.82	145.77
Stenostomum unicolor	7	49	0.0003	0.002	0.00004	7.45	52.14
Nematoda	90	365	0.18	0.72	0.02	8.23	33.36
Oligochaeta	365	365	1.44	1.44	0.13	10.85	10.85
Ostracod	21	35	0.001	0.002	0.00005	25.19	41.98
Plecoptera							
Leuctra	333.5	516	0.001	0.001	0.0002	4.3	6.65
Plecoptera	333.5	516	0.83	0.83	0.1	8.575	8.577
Rotifera							
Cephalodella gibba	7	10	0.0002	0.0002	0.000001	243.33	347.62
Cephalodella megalocephala	7	10	0.0002	0.0002	0.000002	66.36	94.81
Colurella geophila	7	10	0.0002	0.0003	0.000003	81.11	115.87
Colurella	7	10	0.0002	0.0004	0.000004	66.36	94.81
Dissotrocha macrostyla	7	10	0.0003	0.0004	0.00001	23.38	33.4
Embata	7	10	0.001	0.001	0.000004	146	208.57
Encentrum	7	10	0.001	0.002	0.00001	243.33	347.62

App. 6 continued

Euchlanis	30	40	0.0002	0.0003	0.000004	60.83	81.11
Lepadella quadricarinata	30	40	0.0001	0.0001	0.000004	22.03	29.38
Notholca squamule	7	10	0.001	0.001	0.000005	146	208.57
Philodina flaviceps	30	40	0.0002	0.0002	0.000003	60.83	81.11
Proales theodora	7	10	0.01	0.01	0.00003	161.17	230.24
Rotaria rotatoria	30	40	0.0001	0.0001	0.000004	23.07	30.77
Simuliidae	104.2	347.5	0.64	2.12	0.05	13.62	45.42
Tardigrada	91.25	912.5	0.0001	0.001	0.00002	4.58	45.79
Trichoptera	340.5	365	1.88	2.02	0.36	5.2	5.57
Athripsodes	340.5	340.5	0.03	0.03	0.003	11.77	11.77
Hydropsyche pellucidula	340.5	340.5	0.01	0.01	0.004	3.66	3.66
Limnephilus	340.5	340.5	0.21	0.21	0.03	6.43	6.43
Polycentropus	365	730	0.001	0.003	0.0001	9.48	18.95
Psychomia pusilla	340.5	340.5	0.01	0.01	0.001	11.68	11.68
Rhyacophila dorsalis	365	456.3	0.3	0.38	0.01	27.08	33.85
Rhyacophila septentrionis	365	456.3	0.17	0.22	0.01	15.69	19.61
Rhyacophila	365	456.3	0.05	0.06	0.01	4.06	5.07
Silo	340.5	340.5	0.24	0.24	0.04	6.42	6.42
Trichoptera	342.5	342.5	0.002	0.002	0.001	3.52	3.52

Appendix 7. Food resources identified, their position within the four seasonal food webs of the River Lambourn, and number codes.

No.	Basal	No.	Basal cont.
1	*Achnanthes sp.*	48	*Synedra sp.*
2	*Achnanthes lanceolata*	49	*Synedra ulna*
3	*Achnanthidium minutissimum*	50	Algae 1
4	*Cocconeis sp.*	51	Algae 2
5	*Cocconeis pediculus*	52	Algae 3
6	*Cocconeis placentula*	53	Bacteria
7	*Cymatopleura librile*	54	Coarse Detritus
8	*Cymbella sp.*	55	Detritus
9	*Cymbella affinis*	56	Detritus Leaf material
10	*Cymbella laevis*	57	Fine Detritus
11	*Cymbella lanceolata*	58	Plant Material
12	*Diatom sp. 1*	59	Ribbon Fungi
13	*Diatom sp. 2*	60	Seed
14	*Diatoma sp. 1*	61	Stones
15	*Diatoma anceps*		
16	*Diatoma vulgare*		Intermediate
17	*Diploneis sp. 1*	62	Egg 1
18	*Diatom sp. 3*	63	Egg 2
19	*Encyonema*	64	Egg 3
20	*Eunotia sp.*	65	*Agapetus fuscipes*
21	*Eunotia pectinalis*	66	*Alona rustica*
22	*Fragilaria sp. A.*	67	*Assulina sp. (Testacea)*
23	*Fragilaria capucina*	68	*Baetis rhodani*
24	*Fragilaria sp. A.*	69	*Brillia modesta*
25	*Gomphonema 2*	70	*Bryocamptus cuspidatus*
26	*Gomphonema olivaceum*	71	*Bryocamptus echinatus*
27	*Gomphonema parvulum*	72	Chironominae sp.
28	*Gomphonema truncatum*	73	Copepoda
29	*Martyana martii*	74	Cyclopoid copepodite
30	*Melosira sp.*	75	*Cyphoderia margaritacea*
31	*Meriodion circulare*	76	*Elmis aenea*
32	*Navicula sp.*	77	Ephemeroptera sp.
33	*Navicula gregaria*	78	*Eukiefferiella clypeata*
34	*Navicula lanceolata*	79	*Eukiefferiella coerulescens*
35	*Navicula capititata*	80	*Eukiefferiella ilkleyensis*
36	*Nitzschia sp.*	81	*Eukiefferiella sp.*
37	*Nitzschia lineares*	82	*Harpacticoida copepodite*
38	*Nitzschia sigmoidea*	83	*Heleniella ornatocollis*
39	*Pinnularia sp.*	84	*Homochaeta naidina*
40	*Pinnularia abaujensis*	85	*Leuctra fusca*
41	*Placoneis sp.*	86	*Leuctra inermis*
42	*Planothidium sp.*	87	Lumbricid sp.
43	*Rhoicosphenia abbreviata*	88	Lumbriculid sp.
44	*Staurosira sp.*	89	*Lumbriculus variegates*
45	*Staurosirella leptostauron*	90	*Marionina sp.*
46	*Staurosirella pinnata*	91	*Micropsectra sp.*
47	*Surirella sp.*	92	*Nais simplex*

App. 7 continued

	Intermediate cont.
93	Nematode sp.
94	Orthocladiinae
95	*Orthocladius thienemanni*
96	*Orthocladius wetterensis*
97	Ostracod sp.
98	*Paracamptus schmeili*
99	*Polypedilum laetum*
100	*Polypedilum cultellatum*
101	*Prodiamesa olivacea*
102	*Rheotanytarsus sp.*
103	*Serratella ignita*
104	*Simulium sp.*
105	*Tanypodinae sp.*
106	Testacea sp.1
107	Testacea sp.2
108	*Thienemaniella spp.*
109	*Tvetenia calvescens*
110	*Tvetenia discoloripes/veralli*
111	*Tvetenia sp.*
112	*Vejdovskyella comata*
113	Chironomidae sp.
	Top Consumer
114	*Aelosoma hemprichi*
115	*Ancylus fluviatillis*
116	*Bryocamptus pygmaeus*
117	*Bryocamptus vejdovski*
118	*Caenis rivulorum*
119	Ceratopogonid sp.
120	*Cernosvistoviella sp.*
121	*Chaetogaster langi*
122	*Corynoneura coronata*
123	*Corynoneura lobata*
124	*Cricotopus bicinctus*
125	*Cricotopus brevipalpis*
126	*Cricotopus sp.*
127	Cyclopoid sp.
128	*Drusus annulatus*
129	*Ephemera danica*
130	*Eukiefferiella claripennis*
131	*Eukiefferiella gracei*
132	*Eukiefferiella lobifera*
133	*Eukiefferiella sp. 1*
134	*Glossiphonia complanata*
135	*Haplotaxis gordioides*
136	*Henlea sp.*
137	*Hydropsyche pellucidula*
138	*Mystacides azurea*

	Top Consumer cont.
139	*Orthocladius excavatus*
140	*Orthocladius rivulorum*
141	*Orthocladius sp. B*
142	*Orthocladius sp.1*
143	*Orthocladius sp. 2*
144	*Ostracod sp. 2*
145	*Paracladopelma sp.*
146	*Paratrissocladius excerptus*
147	*Parorthocladius nudipennis*
148	*Planorbis sp.*
149	*Polypedilum sp.*
150	*Potamothrix bavaricus*
151	*Potamopyrgus antipodarum*
152	*Rheocricotopus fuscipes*
153	*Sericostoma personatum*
154	*Silo nigricornis*
155	*Stylodrilus sp.*
156	*Symposiocladius lignicola*
157	*Tanytarsus sp.*
158	*Thienemaniella clavicornis*
159	*Thienemaniella majuscula*
160	*Thienemaniella partita*
161	*Thienemaniella sp.E.*
162	*Thienemaniella vittata*
163	*Trichoptera sp.*
164	*Tvetenia sp. A.*
	Predator
165	*Conchapelopia sp.*
166	*Gammarus pulex*
167	Limoniinae sp.
	Top Predator
168	*Apsectrotanypus sp.*
169	*Cottus gobi*
170	Astacidae sp.
171	*Erpobdella octoculata*
172	*Glossiphonia heteroclita*
173	*Limnephilus lunatus*
174	*Macropelopia sp.*
175	*Polycentropus flavomaculatus*
176	*Potamophylax latipennis*
177	*Rhyacophila dorsalis*